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ANNUAL ACTIVITIES AND BEHAVIOR OF A GRIZZLY BEAR (URSUS ARCTOS) FAMILY IN NORTHERN ALASKA

UNIVERSITY OF ALASKA M.S. 1982

# ANNUAL ACTIVITIES AND BEHAVIOR OF A GRIZZLY BEAR (*URSUS ARCTOS*) FAMILY IN NORTHERN ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska

In Partial Fulfillment of the Requirements

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by

James G. Gebhard, B.S.

Fairbanks, Alaska

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ANNUAL ACTIVITIES AND BEHAVIOR OF A GRIZZLY BEAR

(URSUS ARCTOS) FAMILY IN NORTHERN ALASKA

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## ABSTRACT

Behavior of a grizzly bear (*Ursus arctos*) family was examined. Active behavior of the sow consisted of 91.5% foraging, 0.9% nursing, 4.3% travel, 0.2% play, 0.6% disturbance and 2.5% miscellaneous; cub activities were similar but play was 3.5%. Foraging showed seasonal shifts that took advantage of high quality foods, and increased in the fall. Ground squirrel (*Spermophilus parryii*) hunting was most important (for the sow) and in the fall provided 21,000 kcal/day. Nursing was important for cubs in spring and summer but ceased in the fall. Evidence suggests this is typical of sows with young, and that nursing does not resume until the following spring. Travel by the sow was mostly food related. Travel by the cubs served to help maintain proximity to the sow. Play was similar to black bear's (*U. americanus*) but reflected differing environments and lifestyles. Aggression largely involved prized foods. The sow's rest was light and she periodically monitored her surroundings. Seasonal patterns occurred in movements and proximity of family members.

This manuscript is specially dedicated with love to my grizzly family, for the treasured experience of sharing their daily lives. To the three bears - Sarah, Angel, and Dusty - wherever they may be. And to all that's wild and free.

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# INTRODUCTION

The grizzly bear population on the North Slope of the Brooks Range of Alaska is particularly vulnerable to impacts resulting from industrial development. Here the climate is unusually harsh, the summer growth season and period of food availability unusually short, the concentration of food sources relatively poor, the home range size requirements relatively large, reproductive potential low, and concealing vegetative cover sparse. In this region, sows with young hibernate for about 7 months out of the year (Reynolds, 1980).

Within the North Slope, the National Petroleum Reserve in Alaska (NPR-A) is the largest remaining undeveloped area. It is believed to contain oil and gas reserves which are currently being sought. Oil and gas development here almost certainly will increase access and human habitation, disrupt habitat and increase man-bear confrontations.

Adverse interactions which occurred as a result of the development of the nearby Prudhoe Bay oilfield included illegal shooting of grizzlies, attraction of grizzlies to field camps, shooting of "problem bears" habituated to feeding on garbage and human handouts, and harassment from aircraft and surface vehicles (Schallenberger, 1980). The simple awareness of unhabituated bears of the presence of humans is often enough to cause severe disturbance. Noisy human activities have been observed to cause grizzlies to abandon their dens (Quimby, 1974). Development could result in large population declines and even in the eventual eradication of grizzlies from this region if measures are not taken to better understand potential sources of impact on them and to

minimize conflicts with man. Depending on the intensity of development, even this may not suffice.

To obtain a greater understanding of the grizzly population in this region, federal funding was supplied between 1977 and 1979 to the Alaska Department of Fish and Game to perform a baseline biological study of the NPR-A grizzly population. My study, conducted in 1977, complemented this by examining in detail activities and behavior of a single bear family. Activity patterns and behavior of a grizzly family have never been systematically studied before under natural conditions, except for limited observations of specific aspects, such as nursing. The successful rearing of young to become self sufficient members of the grizzly population is a key aspect of the grizzly's life history, and knowledge thereof is important to the successful management of grizzly populations.

Observations were made of an adult sow (16 1/2 years old) with her two yearling cubs (a male, cub 1; and a female, cub 2) during their active period from spring through fall denning. Activities examined included the various shifting feeding patterns, resting patterns, travel, and play. Behavioral analyses were made of nursing, play and aggressive interactions within the family unit. More limited behavioral observations were also made of the various types of feeding activity (such as predation), and of resting, travel, intraspecific interactions with bears outside the family unit, mosquito harassment, and various human disturbances. Movement proximity of family members and home range, were examined.

## STUDY AREA

The study area was centered around Meat Mountain on the North Slope of the Brooks Range within the region designated as the National Petroleum Reserve in Alaska (NPR-A). See Figure 1. NPR-A encompasses about 18,000 $km^2$ (37,000 $mi^2$) and is the size of the state of Maine. Within the NPR-A there are three major physiographic provinces, the Arctic Coastal Plain, the Arctic Foothills and the Brooks Range. The study area lies within the southern section of the Arctic Foothills. Descriptions of the study area are based on Selkregg (1975), U.S.D.I. (1978a), and U.S.D.I. (1978b).

The Arctic Foothills in the NPR-A is characterized by tundra-covered rolling hills, plateaus, and low east-west ridges. Altitudes in the southern section range from 370 m (1,200 ft) in the north to 1,100 m (3,500 ft) in the south where it borders on the Brooks Range. The bear family's home range centered around Meat Mountain, an east-west ridge. Elevations occurring within the home range of the grizzly family ranged from 370 m (1,200 ft) to 880 m (2,900 ft). Permafrost is continuous throughout the NPR-A region and soil drainage is poor. Average annual precipitation ranges from about 130 to 180 mm (5 to 7 in). Snow depth in the Foothills ranged from 250 to 790 mm (10 to 31 in) during the year of this study. Available data on average and extreme air temperatures for the Foothills are limited to records from Umiat. Temperature extremes there range from -53°C to 29°C (-63°F to 85°F). The average monthly minimum temperature over the sow's active year from 7 May through 8 October (as recorded at Umiat) has varied from -18°C (0°F) in October to

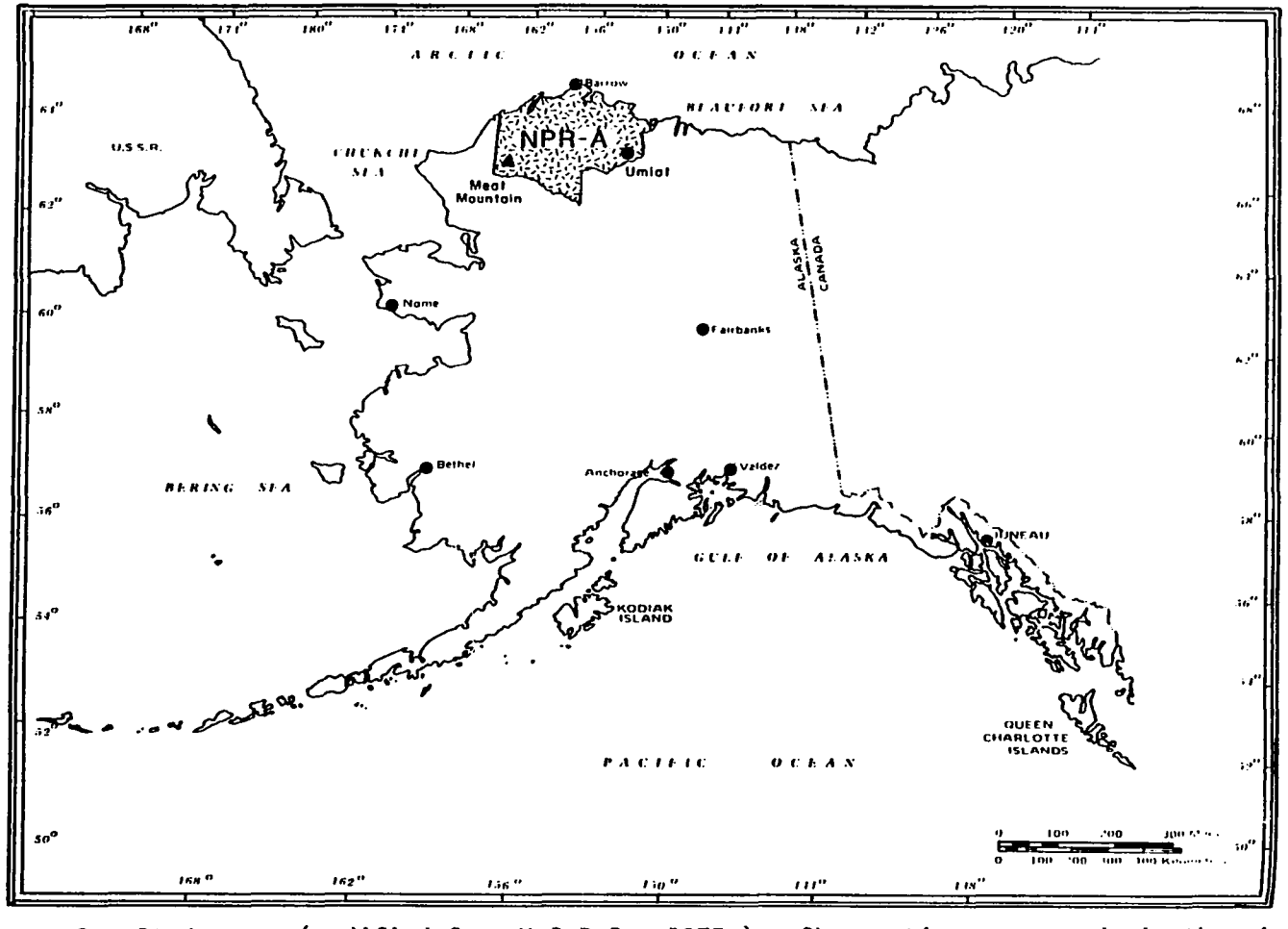


Figure 1. Study area (modified from U.S.D.I., 1975a). Observations were made in the vicinity of Meat Mt.

6°C (43°F) in July and the average maximum temperature from -8°C (17°F) in October to 17°C (62°F) in July. Temperature extremes over this time ranged from -30°C (-22°F) in May to 29°C (85°F) in July.

In the Arctic where it is windy much of the time, wind chill values which reflect the effect of wind on heat loss are more important than air temperature (Searby, 1971). A 16 kph (10 mph) wind at 0°C (32°F) results in heat loss equivalent to -8°C (18°F) and at -18°C (0°F) results in heat loss equivalent to -29°C (-20°F). In the Meat Mountain study area periodic storms occur with winds above 64 kph (40 mph) which may last several days or more. With a 64 kph wind at 0°C (32°F) the equivalent wind chill temperature is -19°C (-3°F) and at -18°C (0°F) is -51°C (-60°F). Wind speeds measured in this study ranged from 0 to 105 kph (0 to 65 mph) with gusts that went higher. Wind speeds were highly variable but most commonly were about 8 to 16 kph (5 to 10 mph). Fog is relatively common in the study area. Monthly average percent frequency of occurrence values from Umiat range from about 7 to 16% between May and October, and values appeared to be even higher in the study area.

The most abundant vegetation type in NPR-A is upland tussock tundra (Spetzman, 1959) which covers a large part of the coastal plain and most of the Foothills up to 900 m (3,000 ft). The Meat Mountain study area is predominantly tussock tundra with associated river valleys, dry alpine tundra ridges, and barren alpine talus areas. The dominant plant species of upland tundra is the tussock-forming cottongrass Eriophorum vaginatum. Tussocks are typically about 150 to 300 mm (1/2 to 1 ft) in both height and width. The tussock community varies from almost pure

cottongrass stands to cottongrass stands dominated by an overstory of low shrubs. Plants associated with cottongrass tussock vary greatly depending on local soil and water conditions, on the degree of slope, and on whether the slope is north- or south-facing. Willow (Salix spp.) thickets dominate along streams and may commonly reach 900 mm (3 ft) in height.

Small mammals occurring in the foothills of NPR-A include 3 species of shrews, 3 species of voles, 2 species of lemmings, the arctic ground squirrel (Spermophilus parryii), and the hoary marmot (Marmota broweri). Ungulates include caribou (Rangifer tarandus), moose (Alces alces), and Dall Sheep (Ovis dalli). Predators include the gray wolf (Canis lupus), arctic fox (Alopex lagopus), red fox (Vulpes vulpes), grizzly bear (Ursus arctos), ermine (Mustela erminea), least weasel (Mustela nivalis), and wolverine (Gulo gulo). All species were directly observed in the Meat Mountain study area as well, except for voles, shrews, lemmings, ermine, and Dall Sheep. The small mammals probably were overlooked due to their small size and/or local scarcity at this time and Dall Sheep were confined to the Brooks Range. The Meat Mountain study area occurs on the outskirts of the calving grounds of the Western Arctic Caribou Herd, and in 1977 caribou were relatively abundant in the area from about late May through mid June.

## OBSERVATIONS

A sow with yearlings was located by the Alaska Department of Fish and Game about 3 weeks after emergence from her den. On the evening of 29 May 1977 she was immobilized with 235 mg of Sernylan, measured and weighed. A lower premolar tooth was extracted for age determination via a cementum layer count (Craighead et al., 1970). She then was further anesthetized using chloroform, and a temperature-sensitive telemetry transmitter was surgically implanted in the back of her neck. She was again immobilized, weighed, and measured and fitted with a radiocollar on 24 June, and was again immobilized, weighed, and measured on 8 August.

With the assistance of another graduate student, John Hechtel, I observed the family group on alternate weeks from first location on 28 May until 15 August. Observations were for 24 hour periods when conditions permitted, and observations were in alternate 4 and 8 hour shifts. The other week in the alternate series was devoted to a vegetation study of the area and mapping of bear habitat, in which I assisted the other graduate student on his project. From 16 August until 30 September, when detailed observations ended, observations were conducted almost entirely by me. Observations were made from first location of the family unit until darkness, weather, or other conditions prevented further observation for an extended period of time. When family members were hidden by terrain, however, as often happened, watches normally were maintained until they reappeared and observations could be continued.

Observations occurred at distances from as little as 45 m (150 ft) to as much as 5.6 km (3.5 mi) using binoculars or, more often, a 15-60x

spotting scope. Observation sites were selected which provided the best available overall view of the surrounding terrain, while at the same time were unlikely to allow the family to become aware of human presence.

Observations of activities were recorded in minutes from the time of first observation of the activity until its cessation and the beginning of a new activity. Times were rounded off to the nearest minute. Activities which lasted less than 30 seconds were not recorded in activity time totals. Some forms of activity, however, which did not normally last 30 seconds (such as aggression), while not recorded in activity time totals, were tabulated as to number of occurrences. During periods of frequent shifting from one activity to another a tape recorder was used to record observations which were transcribed later that day.

Movements and proximity of each family member were recorded on the hour during observation periods. Environmental conditions such as temperature, wind speed, cloud cover, precipitation, and mosquito densities were also recorded on the hour at these times.

The family group was located with portable ground tracking equipment which picked up signals from both the implant and radiocollar of the sow. Lightweight backpacking gear facilitated ground tracking in the fall when extensive movements of the family often required shifting camp every day. When extensive ground tracking failed to locate the family group the main Fish and Game camp was contacted at the earliest opportunity. When time and weather permitted a Supercub equipped with radiotracking equipment (which was being used for a grizzly bear population study by personnel of the Alaska Dept. of Fish and Game) would be sent out to locate the family.

Over the course of the year, the sow was observed for 359 hours, cub 1 for 354 hours and cub 2 for 355 hours. In addition, observations were made in the same area of another sow with 2 spring cubs for approximately 3 hours per family member.

Activity periods of the family group were divided into five seasons:

Spring: May 7 - June 8 (May 28 - June 8)

Early Summer: June 9 - July 8 (June 9 - June 30)

Late Summer: July 9 - August 8 (July 13 - July 17)

Early Fall: August 9 - September 8 (August 9 - September 5)

Late Fall: September 9 - October 8 (September 9 - September 30)

Dates in parentheses are intervals during each season in which actual recorded observations of the family were made. The beginning of the year started with emergence of the family in spring and was estimated to occur around 7 May (Harry Reynolds, pers. comm.). The end of the year occurred on the evening of 8 October or morning of 9 October when the family denned for the year. Early summer began with the emergence of new vegetative growth in early snow-free areas, and corresponded roughly with the first half of the growing season. Late summer corresponded roughly with the second half of the growing season. Early fall was characterized by falling temperatures, a die-off of herbaceous vegetative growth and the presence of an abundance of ripe berries. Late fall was characterized, at least in 1977, by rapidly falling temperatures, a succession of severe storms and a steadily increasing blanket of snow which made movements more difficult and made locating and obtaining food sources a much more laborious chore.

Locating and observing the family became increasingly difficult over the year. This was due to a combination of increased movements by the family group (which made them harder to find) and to increasingly poor visibility conditions during this year. Factors contributing to poor visibility included fog, rain, snow, high winds, smoke and rapidly increasing hours of darkness in the fall.

Despite adverse conditions at times, the undeveloped, open, treeless character of much of the North Slope and the 24 hour periods of daylight from spring through summer, provide outstanding opportunities for observing wildlife in their natural environment at distances that do not interfere with normal behavioral patterns.

## HOME RANGE

### Methods

Home range of the sow during 1977 was calculated with the minimum home range polygon method used by Craighead and Craighead (1972), Pearson (1975, 1976), Craighead (1976), and Reynolds (1980). The seasonal home ranges were calculated by placing seasonal observations of the sow on topographic maps (scale 1:250,000), connecting peripheral locations and calculating the area within. A mylar overlay of seasonal home ranges was made, peripheral locations of combined seasonal home ranges were connected and the home range for the entire year obtained by calculating the area within. Observations were a combination of ground locations by me and aerial observations by the Alaska Department of Fish and Game.

### Results and Discussion

Table 1 shows the observed seasonal and yearly home range size, and because home range size is affected by the number of locations - the number of days located per season (excluding those in which the sow was heavily drugged or recovering from surgery).

Over the year, the sow's home range was similar to that of other sows with young on the North Slope of Alaska, but larger than observed for females elsewhere (Reynolds, 1980). Home range use over most of the year centered around particular areas. These centers of activity usually appeared to be used more heavily because of their higher general availability of preferred food sources, and at times because of the availability

Table 1. Yearly and seasonal home range size of the family group.

| | Area utilized $km^2$ ($mi^2$) | Number of Days Located |
|---|---|---|
| Spring | 6.5 (2.5) | 7 |
| Early Summer | 63.2 (24.4) | 20 |
| Late Summer | 110.8 (42.8) | 15 |
| Early Fall | 115.0 (44.4) | 25 |
| Late Fall | 158.0 (61.0) | 16 |
| Entire Active Year | 244.5 (94.4) | 83 |

of preferred resting sites. Heavily used areas changed seasonally as phenology and availability of food sources changed, and with rest site requirements. The area utilized from late May through most of June was small and largely confined to a narrow area encompassing the base and talus ledges of Meat Mt. Use of this area suggested an attempt to minimize contacts with large boars at a time when the young may have been particularly vulnerable to predation. Centers of activity, after the peak of the breeding season, often were quite large and considerable movement occurred within them. Widespread feeding (both inside and out of centers of activity) probably allowed the sow and her cubs to familiarize themselves with the area, enhanced location of ground squirrel burrows, and maximized chance encounters with particularly high value food sources in general (such as carrion, nesting birds, eggs, feeding ground squirrels, and microhabitats with preferred vegetation). Widespread foraging also minimized damage to any one particular feeding area.

Figure 2 illustrates seasonal home range areas utilized by the sow and cubs. The area utilized was smallest in the spring at which time the sow's movements were largely confined to a relatively small area on the north side of Meat Mountain. Within this small area, activity centered in early snow melt areas along the north facing slope at the base of the mountain where the family foraged for roots, and along the upper shelves of the mountain where resting sites were selected. In early summer the overall observed area utilized increased nearly 10 times that noted in the spring. (It should be noted that the number of days observed was also nearly 3 times that of the spring.) Seasonal home range expanded to encompass the western 2/3 of Meat Mountain. This

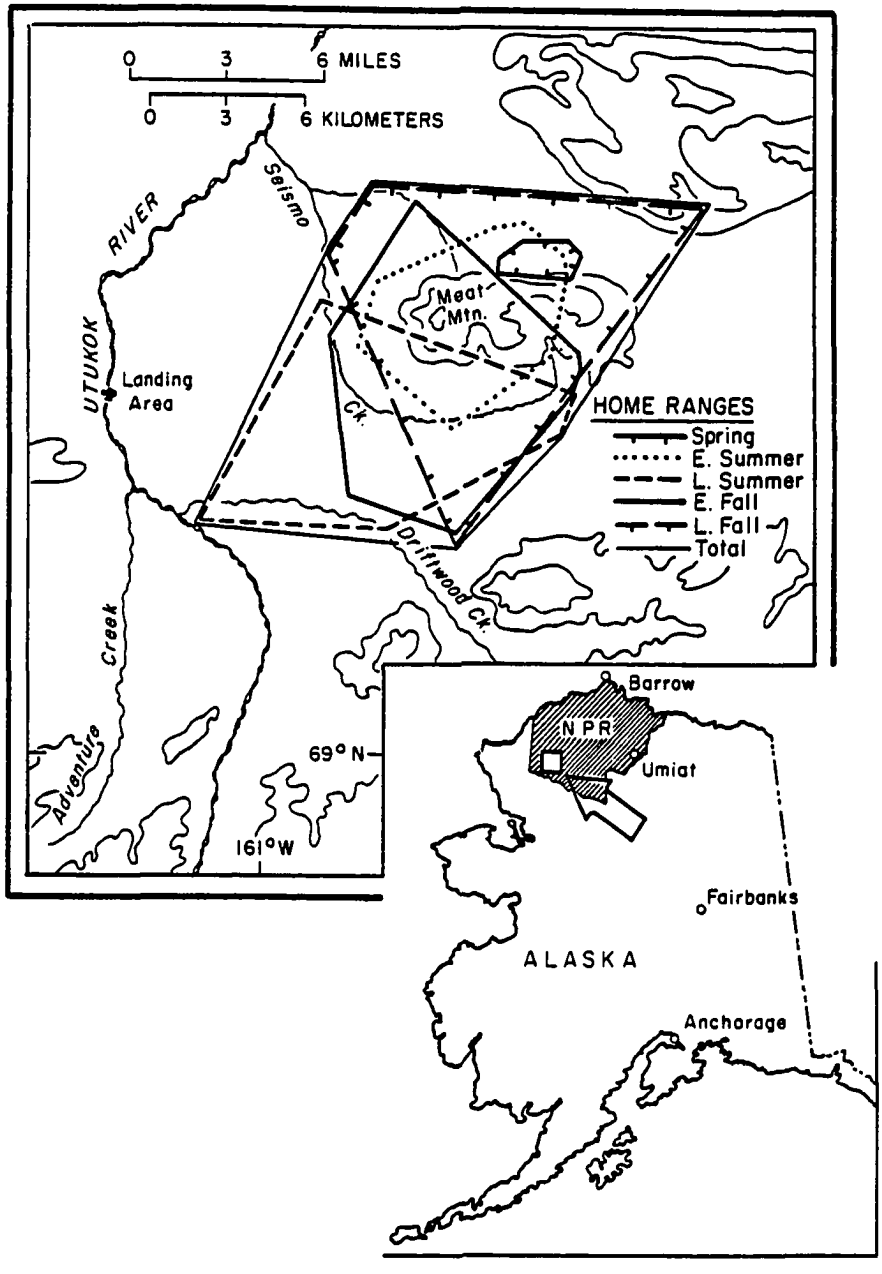


Figure 2. Home Range of the grizzly bear family.

large increase however was due almost entirely to 2 periods of movement during the second half of this season, from 22 June onward, in which 2 repeated circuits of the western 2/3 of Meat Mountain were made. During the first half of the early summer season from 9 June to 21 June, movements were, except for a 3.2 km (2.0 mi) westward extension, confined to the same area noted in the spring where the northern slopes now provided nutritious emerging vegetation and where isolated talus slopes were still available nearby for resting. In this first half the overall area utilized was 12.2 $km^2$ (4.7 $mi^2$) and in the second half was about 57 $km^2$ (22 $mi^2$). (The number of days observed were 9 and 11 respectively.) Activity in early summer occurred predominantly along the base of Meat Mountain and within the major valleys associated with Meat Mountain, where nutritious, emerging vegetation was available.

In late summer the home range increased still farther to nearly double the size of early summer. Late summer home range encompassed a large area from the southern slopes of Meat Mountain, south to the area around Driftwood Creek. Activity between 11 July and 28 July occurred mainly along a 1.6 km (1.0 mi) wide strip along and south of Seismo Creek and extended about 9.7 km (6.0 mi) between the southwestern leg of Meat Mountain and the area west of Meat Mountain where Seismo Creek flows north and, from 31 July to 8 August, mainly along a 9.7 km (6.0 mi) stretch of Driftwood Creek south and west of Meat Mountain. Drainages of various sizes were heavily used. Some drainage areas where snow melted late still provided young vegetation well into late summer, and a few snowbanks were still available there for resting.

In early fall observed total home range area remained about the

same as in late summer. From the first part of early fall through 18 August, activity was confined to a 17.4 $km^2$ (6.7$mi^2$) area along the southwest slopes of Meat Mountain (days observed = 10). After this period movement increased considerably and home range size for the remainder of early fall increased considerably. Home range size was 115 $km^2$, the same as for the entire early fall period (days observed = 15). The extended movements of this period somewhat resembled those occurring in late fall. While excursions of 2 to 3 days to other areas did occur in the latter half of early fall, activity during the entire early fall period occurred mostly along a very broad area extending from the gentle slopes along the south side of Meat Mountain, down to the bluffs along the south side of Seismo Creek. Many berries and ground squirrels occurred in this area and an unusually high density of ground squirrels occurred along the bluffs south of Seismo Creek.

In late fall overall home range size increased by roughly 40% over that of late summer and early fall and reached its highest seasonal value. Large areas were covered almost every time the bears were observed and a variety of areas were visited and utilized. This behavior may have been partially due to (1) a gradual blanketing of vegetation with a deepening layer of snow (which reduced accessibility of vegetable matter in most areas), and (2) an increasing search for ground squirrel burrows. In the first part of late fall larger drainages, which tended to melt lesser snow falls, were utilized more heavily, probably because less energy was required for movements and the relative ease of locating and consuming berries. The gently rolling slopes of the western 2/3 of Meat Mountain were used more heavily during the week and a half prior to denning on a northwestern slope of Meat Mountain.

## RESTING VERSUS ACTIVE BEHAVIOR PATTERNS

### Methods

A bear was considered to be resting when lying or sitting and not engaged in any other activity (such as feeding, watching and waiting as the sow dug ground squirrels, or play). Active behaviors were divided into feeding/foraging behavior, travel, play, aggression, disturbance and miscellaneous activities.

The total directly-observed time spent in each active category was tabulated for each family member both seasonally and yearly as was the percent of directly observed total active time for each category except aggression, in which total time spent was negligible. Values for the sow in the spring season exclude the three day period when she was recovering from immobilization and surgery, because the active behaviors engaged in during this time appeared not only greatly reduced in overall extent but greatly changed in relative proportions as well. Values for the cubs included this period, however. Although the level of active behaviors for cubs was somewhat reduced, overall the proportion of active behaviors was relatively unchanged. Inclusion of this period for the cubs has the advantage of greatly increasing sample size.

Resting tended to be underrepresented as a directly observed (D.O.) activity. This was largely a result of the bears being less visible when resting since they were much more easily obscured by vegetation and surrounding terrain when lying down and less easily distinguished when motionless. In addition, the sow, during parts of the year, selected resting sites particularly difficult to view. To reduce this bias,

instances when it was virtually certain that resting was occurring almost all of the time were included in a special category - indirectly observed (I.O.) resting. These instances included any in which a bear was observed to lie down and was fully or partially hidden as a result and was observed later to reappear in the same area, and those instances where a bear moved into a small hidden area for more than 30 minutes where it was unlikely it could have moved about or fed for more than a minute without being seen, and was observed to emerge from the same small area much later. Indirectly observed resting almost certainly included some time actually spent in nursing since nursing was usually associated with resting but since the proportion of time nursing was very small compared to resting this was ignored. Other possible sources of error may have been an occasional short period of play between the cubs or an infrequent minute of feeding that may have been included in indirectly observed (I.O.) resting. The indirectly observed (I.O.) resting totals were combined with directly observed (D.O.) resting totals for comparison with active totals.

An estimate was made of indirectly observed (I.O.) active periods. Such periods included instances when a bear was grazing or traveling but was hidden for short periods and reappeared a distance away along the same line of movement, still feeding or traveling. The D.O./I.O. active period totals were combined for comparison with the resting total.

In comparing combined overall resting totals with combined overall active totals, data for the spring season are shown both with and without the inclusion of the 3 day recovery period following the sow's minor surgery. Inclusion of this period severely biases the data for the sow

who spent practically the entire 3 days resting. Inclusion of this period also biases the proportion of overall time spent resting to the overall time spent active for the cubs to some extent since the cubs normally tended to associate their activity patterns with that of the sow - and therefore tended to rest more than usual at this time. Values based on spring data excluding this period would therefore seem more accurate for the entire family even though the data base for this season is much more limited without it. Spring data without this period are used here for comparison with other seasons. These spring active percentages, however, probably are on the high side because the sow usually traveled to high talus ledges to rest in the spring and at times could not be relocated again until she moved back down to the flats and resumed activity. Questionable incidents such as this were not tabulated.

## Results and Discussion

Active behaviors (Table 2) consisted of feeding/foraging activities, travel, play, aggression, disturbance and miscellaneous activities.

Feeding behavior was by far the most important active category even though it was underrepresented because it only included actual feeding and foraging behavior and not other related behaviors. Most of travel time, for instance, was related to movements between feeding places; nursing by the sow involved feeding the cubs and was not included in feeding for her since she herself was not actually feeding or foraging; miscellaneous activity for the sow in early summer was largely related to covering up a caribou carcass and did not fall into the category of

Table 2. Yearly and seasonal active behaviors of the family group (percent and minutes).

| Percent (%) | Feeding/ Foraging | Nursing | Travel | Play | Distur- bances | Miscel- laneous |
|---|---|---|---|---|---|---|
| Sow | | | | | | |
| Spring* | 94.3 | 1.7 | 2.7 | - | 0.6 | 0.8 |
| Early Summer | 81.2 | 2.1 | 7.3 | 0.7 | 1.4 | 7.4 |
| Late Summer | 97.0 | 0.3 | 1.7 | 0.1 | 0.0 | 1.0 |
| Early Fall | 94.2 | 0.5 | 3.9 | 0.0 | 0.5 | 0.9 |
| Late Fall | 86.6 | - | 10.4 | - | 1.1 | 2.0 |
| Entire Active Year* | 91.5 | 0.9 | 4.3 | 0.2 | 0.6 | 2.5 |
| Cub 1 | | | | | | |
| Spring* | 95.4 | - | 2.2 | 0.6 | 0.5 | 1.3 |
| Early Summer | 80.3 | - | 6.4 | 10.1 | 1.1 | 2.0 |
| Late Summer | 93.6 | - | 2.0 | 3.2 | 0.0 | 1.2 |
| Early Fall | 93.7 | - | 3.8 | 1.2 | 0.5 | 0.8 |
| Late Fall | 79.3 | - | 8.7 | 1.3 | 0.9 | 9.7 |
| Entire Active Year* | 90.4 | - | 3.9 | 3.5 | 0.5 | 1.7 |
| Cub 2 | | | | | | |
| Spring* | 97.0 | - | 1.9 | - | 0.6 | 0.5 |
| Early Summer | 79.7 | - | 7.3 | 10.4 | 1.2 | 1.4 |
| Late Summer | 94.0 | - | 1.8 | 3.1 | 0.0 | 1.1 |
| Early Fall | 93.6 | - | 4.0 | 1.3 | 0.5 | 0.7 |
| Late Fall | 75.1 | - | 11.3 | 1.4 | 1.0 | 11.3 |
| Entire Active Year* | 90.5 | - | 4.1 | 3.3 | 0.6 | 1.4 |

Table 2. Continued.

| Minutes | Feeding/ Foraging | Nursing | Travel | Play | Distur- bances | Miscel- laneous |
|---|---|---|---|---|---|---|
| Sow | | | | | | |
| Spring* | 1021 | 18 | 29 | - | 6 | 9 |
| Early Summer | 2088 | 53 | 187 | 17 | 35 | 191 |
| Late Summer | 2929 | 9 | 50 | 3 | 1 | 29 |
| Early Fall | 3662 | 20 | 150 | 1 | 21 | 35 |
| Late Fall | 575 | - | 69 | - | 7 | 13 |
| Entire Active Year* | 10275 | 100 | 485 | 21 | 70 | 277 |
| Cub 1 | | | | | | |
| Spring* | 2349 | - | 55 | 16 | 12 | 31 |
| Early Summer | 2183 | - | 175 | 274 | 30 | 54 |
| Late Summer | 2666 | - | 56 | 91 | 1 | 33 |
| Early Fall | 3628 | - | 148 | 48 | 18 | 30 |
| Late Fall | 530 | - | 58 | 9 | 6 | 65 |
| Entire Active Year* | 11356 | - | 492 | 438 | 67 | 213 |
| Cub 2 | | | | | | |
| Spring* | 2322 | - | 46 | - | 14 | 12 |
| Early Summer | 1988 | - | 181 | 260 | 30 | 34 |
| Late Summer | 2661 | - | 50 | 88 | 1 | 32 |
| Early Fall | 3573 | - | 154 | 48 | 18 | 25 |
| Late Fall | 474 | - | 71 | 9 | 6 | 71 |
| Entire Active Year* | 11018 | - | 502 | 405 | 69 | 174 |

*Spring and yearly active times for the sow excluded the immobilization and recovery period, which affected the proportions of time spent in various active behaviors by the sow. This period is included in data for the cubs since it did not affect the proportion of time they spent in the various active behaviors tabulated here.

actually feeding or foraging. Also borderline activity which could not be clearly distinguished as feeding or traveling was classified as miscellaneous. Individual activity categories are discussed in detail in later sections.

Yearly and Seasonal Patterns of Overall Activity

Total minutes and percentage of resting versus active time are compared in Table 3 on both a yearly and seasonal basis for each family member.

Activity levels remained roughly the same during spring, early summer, and late summer seasons and then increased substantially in early fall and again in the late fall. From late summer to late fall behavior of the sow increased from 59% active to 85% active. This large increase in activity, which started around the end of the growing season was almost entirely food related. The sow and cubs were active roughly 14 hours per day in spring, early summer and late summer seasons, 17 hours per day in early fall and 20 hours per day in late fall. Values for the cubs were similar.

The actual increase in activity began during mid-early fall. If the year is redivided accordingly, the family was active roughly 14 hours/day from spring through mid-early fall and 22 hours/day (92% active) during the remainder of the fall (based on 10,000 sample minutes for all family members combined and 3330 for the family as a unit). Activity was slightly greater in the second half of early fall than in late fall, possibly due to the small sample size in late fall. Fall activity levels are based on the assumption that activity continued nocturnally at similar levels as during the day. This assumption seems

Table 3. Yearly and seasonal active and resting proportions of the family group

| | Percent (%) | | | | | |
|---|---|---|---|---|---|---|
| | Sow | | Cub 1 | | Cub 2 | |
| | Resting | Active | Resting | Active | Resting | Active |
| Spring | 69.4 | 30.6 | 47.3 | 52.7 | 49.1 | 50.9 |
| Spring* | 39.5 | 60.5 | 36.4 | 63.6 | 39.3 | 60.7 |
| Early Summer | 42.8 | 57.2 | 38.5 | 61.5 | 43.1 | 56.9 |
| Late Summer | 41.1 | 58.9 | 42.0 | 58.0 | 42.7 | 57.3 |
| Early Fall | 28.5 | 71.5 | 28.2 | 71.8 | 29.5 | 70.6 |
| Late Fall | 14.7 | 85.3 | 15.2 | 84.8 | 19.4 | 80.4 |
| Entire Active Year* | 36.0 | 64.0 | 34.8 | 65.2 | 37.0 | 63.0 |
| Entire Active Year | 42.8 | 57.2 | 37.4 | 62.6 | 39.5 | 60.5 |

*Excludes the 3-day recovery period.

(percent and minutes).

| Minutes | | | | | |
|---|---|---|---|---|---|
| Sow | | Cub 1 | | Cub 2 | |
| Resting | Active | Resting | Active | Resting | Active |
| 3308 | 1417 | 2214 | 2463 | 2310 | 2394 |
| 708 | 1083 | 652 | 1139 | 723 | 1119 |
| 1972 | 2640 | 1754 | 2799 | 1954 | 2575 |
| 2141 | 3073 | 2114 | 2914 | 2161 | 2899 |
| 1797 | 4514 | 1745 | 4435 | 1824 | 4370 |
| 117 | 680 | 121 | 677 | 154 | 641 |
| 6735 | 11,990 | 6399 | 11,964 | 6816 | 11,604 |
| 9235 | 12,324 | 7948 | 13,288 | 8404 | 12,879 |

valid for 2 reasons. First, the family was active until darkness and was typically found active at first light, usually a substantial distance away from the last sighting. Second, average hourly point-to-point movements of the family during this period, when examined in conjunction with the extensive overnight movements suggests the family was generally active throughout much and possibly all of the night. Data on overnight movements is limited however, and it is possible that activity levels may have increased or decreased somewhat during nocturnal hours. If so, fall activity levels may be somewhat higher or lower than projected here.

Increases in fall activity have been noted elsewhere. Craighead (pers. comm. cited by Nelson, 1978) observed that grizzlies in the wild fed 20 hours per day in late fall (and consumed upwards of 20,000 kcal/day). Sizemore (1980), who studied activities of 4 radiocollared grizzlies, found all were more active during the period from 1 August to den entry than from den emergence to 31 July.

Daily Patterns in Durations of Activities

Daily patterns of activity appeared to involve 3 basic patterns in terms of active versus resting periods. The first involved highly mixed patterns of alternating rest and activity that were often quite variable in duration over the 24 hour periods. This pattern occurred from first observations in late spring until nearly the end of June. By late summer a second pattern had emerged which was largely made up of longer, more continuous periods of alternating resting or active behavior with an especially long period of resting consistently observed from early

afternoon until early evening. During the daylight hours of the first half of early fall a nearly identical pattern was observed, although in early and late fall, increasing darkness severely reduced observations. The long resting period consistently noted in the afternoon from about the end of June may have been a result of avoidance of the hottest portion of the day during the much warmer summer period and possibly to avoidance of high mosquito densities, which were at their peak during these hours in late June and through July. The third pattern, observed from the second half of early fall through late fall, was made up mostly of long periods of activity with interspersed short, sporadic periods of resting. Steadily increasing hours of darkness limited observations at this time and it is possible that a somewhat different pattern may have occurred nocturnally. This third pattern coincided with several other behavioral changes as well.

These broad patterns also show up, though to a lesser extent, seasonally in the length of directly observed resting periods. Uninterrupted resting periods (those without breaks of 30 seconds or more) for the sow averaged 38 minutes in the spring, 50 minutes in early summer, 67 minutes in late summer, 73 minutes in early fall, and dropped to 14 minutes in the late fall. During the first half of early fall the resting period averaged 113 minutes and from the second half of early fall through late fall the resting period averaged 26 minutes.

Yearly and Seasonal Patterns in Hourly Activity Levels

The percentage of time the family group was active during each hour of the day was graphed yearly and seasonally (Fig. 3, a-l). Over the

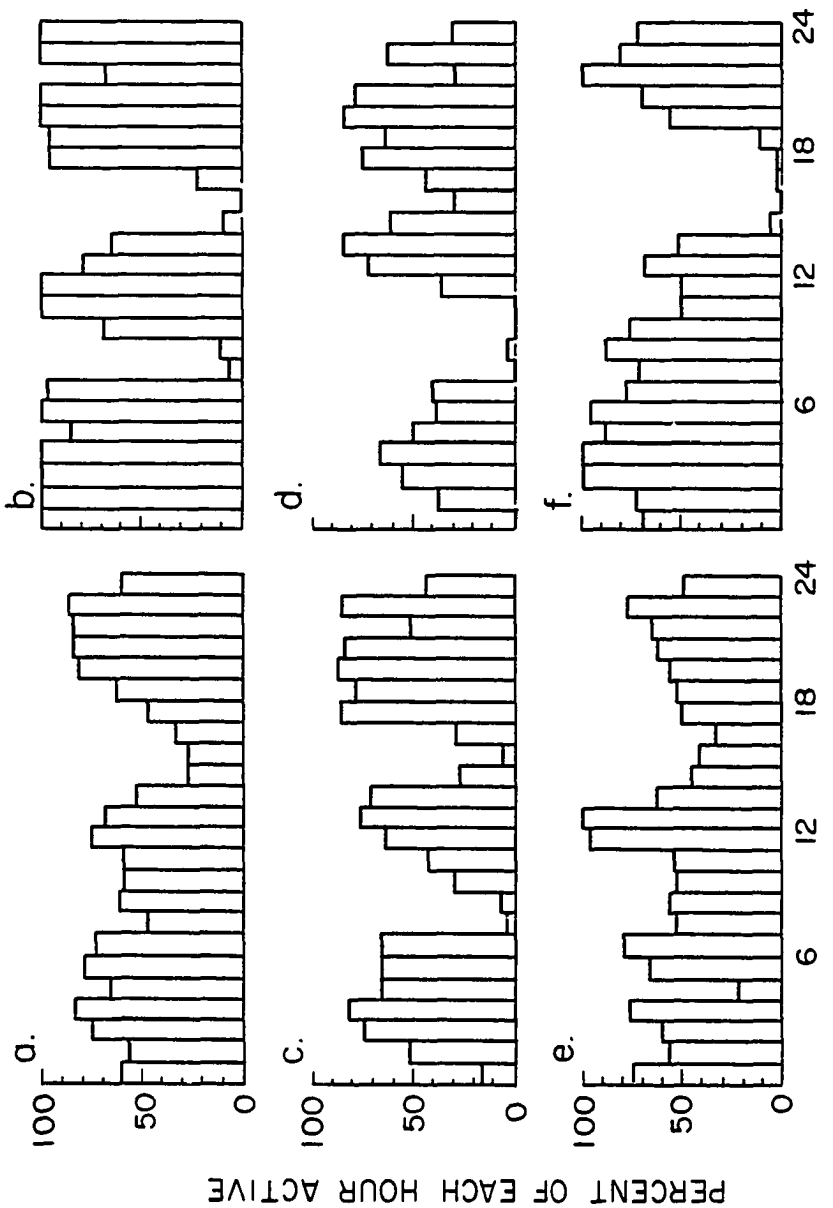


Figure 3. Daily activity patterns of the family group: (A) Entire active year, (B) spring (excluding family activity during the sow's recovery period), (C) spring (excluding the sow's activity during her recovery period), (D) cubs' activity during the recovery period, (E) early summer, (F) late summer, (G) early fall, (H) first half of early fall, (I) late fall, (J) second half of early fall through late fall, (K) summer, (L) fall.

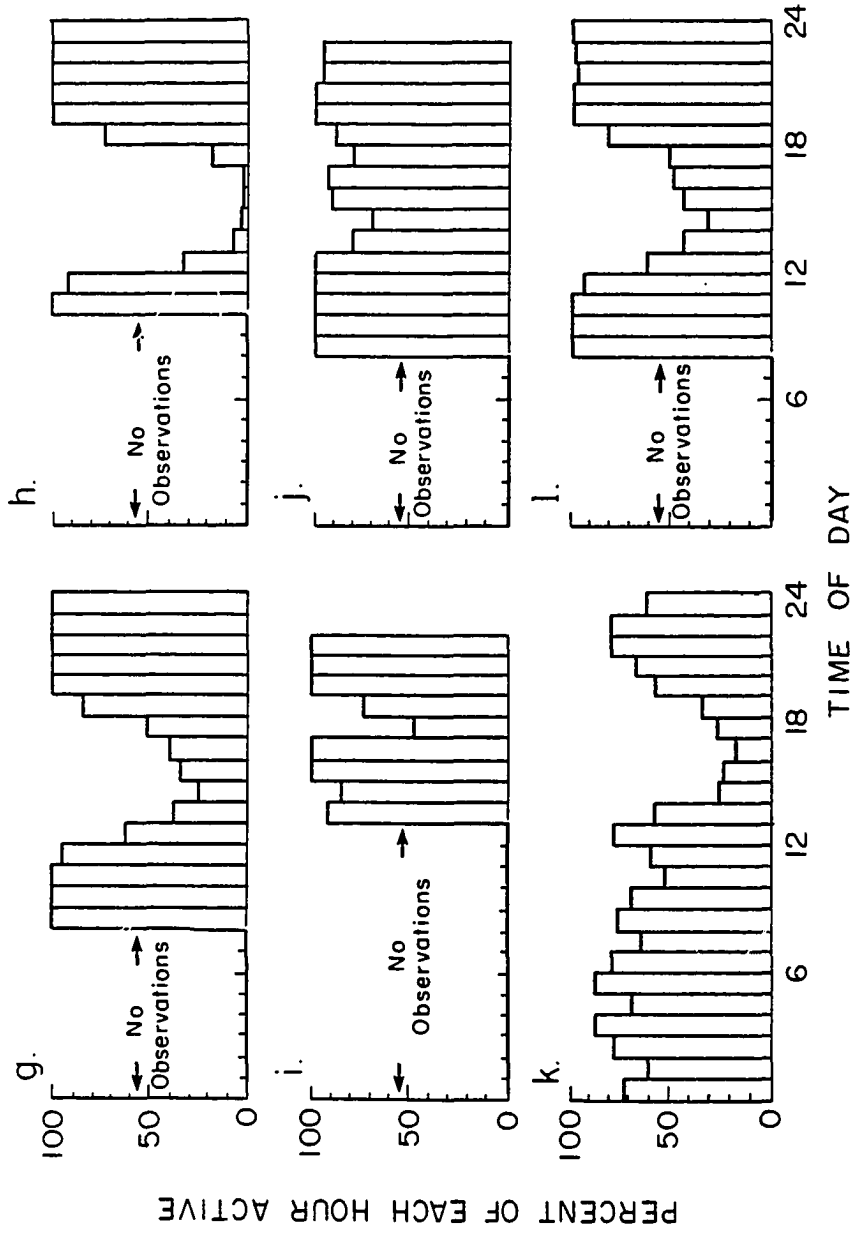


Figure 3. (continued)

year the pattern that emerged was one of increased activity in the early morning hours (after a less active period around midnight) and somewhat increased activity at mid-day followed by a substantial decrease in activity during the afternoon hours with a substantial increase in activity following in the evening (Fig. 3a). The longest, lowest levels of activity occurred in mid to late afternoon and the highest, most sustained daily peak occurred immediately following in the evening.

Figure 3b shows the daily activity patterns in the spring for the entire family group, excluding the 3 day recovery period; Figure 3c for the entire family group excluding data only for the sow during her 3 day recovery period; and Figure 3d the cubs' activity patterns during the sow's 3 day recovery period. During spring without the recovery period (Fig. 3b) sample sizes were very small, especially so during the late night and early morning hours when hourly intervals were often limited to a single hourly sample. During the sow's recovery period the level of activity of the cubs was somewhat reduced overall but the activity types were little changed. The overall daily pattern of the cubs at this time (Fig. 3d) was similar in pattern to the remainder of the spring without the sow's recovery period even though during the sow's recovery period the cubs were largely on their own and no longer constrained to follow the sow's patterns. Because the patterns were similar and the hourly intervals for spring (excluding the recovery period) were so limited for a large portion of the day, the daily activity patterns of the cubs during the sow's recovery period were combined with that of the family group during the rest of the spring season to obtain the overall spring activity pattern (Fig. 3c), and in combination with the

other seasons, to establish the yearly activity pattern throughout the day. This served to increase the sample size of the spring season to a level roughly equal to that of early summer, late summer and early fall seasons in its overall contribution to the yearly pattern - leaving only late fall substantially underrepresented in its contribution to the overall yearly pattern. During the spring, peaks in activity occurred in the early morning, mid-day and in the evening. Troughs, narrower in extent than the peaks, occurred around mid-morning, mid-afternoon and possibly midnight.

In early summer (Fig. 3e), active and resting behavior appeared more spread out over most of the 24 hour period than in spring. The early morning peak observed in spring was considerably flattened. The mid-day peak did however reappear quite strongly in early summer and was again followed by a afternoon decline. While activity again peaked in the evening its rate of increase was gradual and was more moderate in extent than occurred in spring.

In late summer (Fig. 3f) heightened activity again occurred in the early morning hours declining gradually overall until early to mid-afternoon and then dropping off rapidly again in the usual mid through late afternoon activity slump with little or no activity occurring through this period. A high evening peak again followed the slump.

In early fall (Fig. 3g) hours of observation became more limited; observations were reduced to the daylight hours following relocation of the family unit. Earliest observations were nearly at first light and continued as late as midnight under favorable conditions. Active behaviors were at a peak from first observation. A decrease began to occur

around mid-day and became a part of the mid to late afternoon decline noted in the previous seasons. The afternoon drop was again followed by the evening peak in active behavior noted in previous seasons and continued unabated until the family was obscured by darkness. It is uncertain whether active behavior continued during the night but evidence suggests this to be the case for much if not all of the night, at least for the second half of early fall. In early fall a transition also occurred which is not readily apparent from Figure 3g. During the first half of early fall (to about the 24th of August) the pattern observed during the daylight hours (Fig. 3h) was very similar to that of late summer in that a definite resting period of comparable duration occurred in the afternoon, but began an hour earlier. In the second half of early fall (shortly after cessation of nursing) this dramatic afternoon decline in active behavior suddenly shifted to only a modest decline of shorter duration, more reminiscent of late fall.

In late fall (Fig. 3i) the extensive afternoon decline of late summer and the first half of early fall became a narrow dip in the overall active behavior observed during the limited daylight hours. Sample sizes of hourly intervals were small during this season as a result of a succession of extreme storms and the extensive movements of the family group which made daily location much more difficult and time consuming. Figure 3j shows the daily activity pattern with the similar second half of early fall season and late fall season combined.

Figures 3k and 3l show daily activity patterns for the family group for combined summer seasons and combined fall seasons, respectively, for the family group. These figures allow comparisons of activity patterns

observed here with those observed by Stelmock (1981) for spring, summer and fall seasons in Denali National Park, Alaska. Overall seasonal patterns are quite dissimilar for the spring and summer and may in fact suggest an inverse relationship over most of the day. Because the study areas are relatively similar in climate, topography, and light regimes, it might be expected that the daily activity patterns would be similar. The differences in behavior may be due to the sex and reproductive status of bears studied. I observed a sow with young which appeared to be avoiding contacts with other bears, particularly adult males during spring and early summer, while Stelmock (1981) examined activity patterns of all age and sex classes combined. During fall the sow's daily patterns became somewhat more like that of the population observed by Stelmock (1981).

If the sow's activity pattern is representative of family groups in general in far northern climates (rather than simply reflecting her individual preferences), and these differing activity patterns for family groups versus individuals does in fact hold true certain implications are suggested for grizzly bear population studies. Because grizzlies are much easier to locate when active, certain times of day would appear to be much better than others during the various seasons for optimum location of family groups as opposed to individual bears for censusing, immobilization or other management purposes. By choosing certain hours for attempts to locate bears, location of females with young could be optimized or minimized. And by choosing certain other hours, especially in the fall when all bears appear to be active during certain portions of the day, a more representative population sample could be obtained.

## RESTING AND ASSOCIATED BEHAVIORS

The resting pattern and proportion of time spent resting discussed in the preceding section will not be reiterated here and only additional aspects will be discussed.

Resting periods of the sow and each cub showed a broad overlap and were largely coincident with each other. Typically the members of the family unit rested either in contact with, or close to, each other. The cubs appeared to prefer contact with the sow or one another while the sow showed no similar preference and unlike the cubs appeared to make no special effort to rest in this manner. The sow, in fact, would occasionally shift from her original resting site to an alternative one in response to a cub coming over to her and lying next to her. The sow also seemed somewhat more prone to get up and shift to another resting site during a resting period if one or both of the cubs were resting beside her. The cubs in turn usually would get up and move to the sow, though occasionally they shifted to lie by each other instead. The reason for the sow's behavior may have been that the cubs easily disturbed the sow's rest and she generally preferred to maintain a little distance between herself and the cubs.

Throughout the year the sow usually chose dry, vegetated areas with a view of the surrounding terrain for resting. Other than this no site preference pattern appeared to exist throughout the entire year. For some seasons, however, patterns did emerge. In the spring and through most of early summer, the sow most commonly utilized terraced talus ledges along the slopes of Meat Mountain for resting. The sow usually

travelled specifically to these areas from her feeding area along the base of the mountain when she rested for more than a very short time. Only occasionally would she rest at the base of the mountain near her feeding area and only rarely out on the tundra - and then only when drawn by an important prize food source such as a caribou carcass. The sow was not observed to reuse the same site except when she remained in a small area while consuming a large carcass. Ledge sites probably were chosen for their relative dryness and shelter from cold winds, and for their isolation and security from large, aggressive, often cannabilistic boar grizzlies who were covering large areas in search of food and breeding females. Large adult boars are considered the most important source of mortality to cubs and subadults in the study area and have been known to kill and consume adult nonbreeding females with young as well (Reynolds, 1980). Intraspecific mortality caused by adult males has also been documented elsewhere in Alaska (Troyer and Hensel, 1962, 1969; Miller, 1972; Reynolds, 1974, 1976) and in Canada (Pearson, 1975, 1976). Murie (1981) observed a similar use of mountain ledge and cliff areas for resting by family groups during the breeding season in May and June which he attributes to avoidance of adult males which "sometimes attack cubs...". Pearson (1975) notes sows with cubs to utilize areas "as rugged and isolated as possible, particularly in the spring and early summer."

Talus slope ledges were an ideal place for the sow to avoid contact with other bears since little or no food was available to attract other bears into the area and scents of her family unit would be lost or obscured in the windy cross currents occurring on these rugged terraced

ledges, making detection difficult. One closely examined talus ledge site utilized was located on a ledge nearly at the top of Meat Mountain and consisted of a 2 m (7 ft) round hollow with an 2 m (8 ft) long, 1 m (2 1/2 ft) high oblong boulder in front which sheltered the bears from the wind. The sow rested in the hollow, oriented parallel to the boulder, with both cubs lying in contact with the sow and each other at the sow's rear.

In late June, resting sites became more variable as the sow expanded her feeding range. Sites chosen were usually handy to her latest feeding area and dry valley areas and areas adjacent to creeks became more frequently used. By the beginning of late summer the sow often sought out isolated snowbanks along creeks for resting during the hot mid-day, apparently to avoid the heat and mosquitos. These snowbanks were the most heavily used sites from at least early mid-July until the last snowbank in the area melted between 25 and 27 July. This last snowbank was used repeatedly by the sow. Non-snowbank areas along creeks were also used heavily during late summer as alternative resting sites. Tussock valley areas were utilized less commonly as resting sites even though they were used extensively for feeding. Mountain ridges were seldom utilized for resting at this time. In early fall areas adjacent to creeks and sites along the base or slopes of knolls in tussock valleys were the most commonly utilized sites. Resting places appeared to simply be dry comfortable spots within the feeding area. Resting sites in late fall appeared to be similar to those utilized in early fall.

Resting was characterized by a bear occasionally lifting its head to look around and/or scent the air. During the caribou calving season

the sow was timed on one occasion for a period of 30 minutes. During that time she raised her head 13 times, keeping her head raised a total of 135 seconds (av. 10 seconds, range 2-35 seconds). Periods between head raises averaged around 2.3 minutes. During a more normal period in the early summer the sow raised her head 5 times over a 30 minute period for a total of 97 seconds (av. 19 seconds, range 2-65 seconds). The interval between head raises averaged around 6 minutes. In the fall another 30 minute period was also timed. During this period the sow only raised her head 3 times for a total of 30 seconds (av. 10 seconds, range 5-15 seconds). Periods between head raises averaged 8.3 minutes and ranged from 3 to 13 minutes. While the sow would sometimes rest with relatively little head raising it was a fairly consistent component of her resting behavior. These instances illustrate the frequent breaks in the sow's sleep pattern which appeared to be due to a periodic monitoring of her environment. This frequent monitoring served both as a defense against surprise by potential enemies such as large boars and man, and to make the sow aware of potential food items in her area. It was apparent from the few quantified occasions noted and from the many unquantified occasions observed that the sow regulated the frequency of her monitoring, based on feedback from her environment. During the caribou calving season for instance, when caribou were constantly moving through the area and provided a potential source of food, the sow's monitoring frequency was much greater than normal. Similarly, if there was unusual activity in the area such as a plane flying around the area or another bear feeding in the area, the sow's monitoring frequency usually would increase. While sometimes the sow's monitoring level

would increase without apparent reason this was probably generally due to smells or sounds in her environment which went unnoticed by the observer.

Equally apparent from the sow's monitoring behavior was the nature of her rest which appeared typically to take the form of a succession of contiguous cat naps rather than prolonged periods of sleep. While the sow's sleep appeared to be very light during most of these naps, the depth of sleep may have been highly variable. At times, the sow seemed easily disturbed from her rest by even the most minor of disturbances such as a cub lying beside her or shifting position slightly, or even the sound of a very distant plane. At other times she appeared oblivious to much more disturbing behavior, such as play between the cubs as they lay beside her. It is unclear whether the sow at these times was in fact deeply asleep and oblivious to the cubs antics or whether she was simply ignoring them.

While the cubs seemed to follow the general sleep pattern of the sow, the cubs when resting in proximity with the resting sow, would usually be less interrupted by monitoring behavior, and they generally appeared relatively unalert. The most notable exception to this occurred when caribou were nearby and the cubs - especially cub 1 - frequently spent much more time monitoring the caribou than the sow. This was especially true when caribou were nearby well after the calving season when the sow appeared to recognize their relative invulnerability but the cubs did not. On occasions when the cubs rested while the sow continued to feed, the cubs' rest periods often were interrupted by monitoring behavior which served to keep tabs on the sow and, if the other cub was up and about, on the other cub as well.

Resting periods tended to be quite variable and the average continuous resting period relatively short. The term 'continuous' as used here refers to having no active behavioral interruptions of 30 seconds or more within a resting period; alert head raise monitoring (from a lying or sitting position) was considered to be a part of resting behavior. These rest periods averaged about 49 minutes for the sow over the year and about 46 minutes for each cub (Table 4). Rest periods would have been much shorter if head raise monitoring and active behaviors of less than 30 seconds were also counted as breaks. Resting periods were frequently broken up by nursing, by travel to a new resting place, moving off to relieve themselves, or by miscellaneous activity such as standing up to look around and scent the air. The resting periods of the cubs were also at times broken up by play bouts. If breaks due to nursing and other activities of 3 minute duration or less are excluded, the average resting period increases to 69 minutes over the year for the sow. Average resting periods for the cubs were somewhat less. While much longer periods of rest did occur, especially during the afternoon and early evening from late June through mid to late August, these were offset to a large degree in the averages by very short rest periods which often occurred sporadically during feeding activity. Seasonal averages for each family member are tabulated in Table 4. Average seasonal resting periods for the cubs were slightly shorter than for the sow.

Table 4. Yearly and seasonal average durations (minutes) of rest periods for the family group.

| | Continuous[+] Rest Periods | | | Discontinuous[++] Rest Periods | | |
|---|---|---|---|---|---|---|
| | Average | Range | n | Average | Range | n |
| Sow | | | | | | |
| Spring* | 38 | 4-147 | 12 | 57 | 6-152 | 8 |
| Early Summer | 53 | 1-143 | 38 | 62 | 1-363 | 31 |
| Late Summer | 67 | 1-183 | 11 | 105 | 1-334 | 7 |
| Early Fall | 73 | 1-230 | 19 | 126 | 1-354 | 11 |
| Late Fall | 14 | 10-20 | 4 | 19 | 10-31 | 3 |
| Entire Active Year* | 49 | 1-230 | 84 | 69 | 1-363 | 60 |
| Cub 1 | | | | | | |
| Spring* | 29 | 1-138 | 14 | 44 | 2-138 | 9 |
| Early Summer | 39 | 1-275 | 38 | 44 | 1-275 | 34 |
| Late Summer | 64 | 1-181 | 11 | 71 | 1-203 | 10 |
| Early Fall | 78 | 2-227 | 16 | 125 | 14-315 | 10 |
| Late Fall | 12 | 2-24 | 5 | 12 | 2-24 | 5 |
| Entire Active Year* | 46 | 1-275 | 84 | 57 | 1-315 | 68 |
| Cub 2 | | | | | | |
| Spring* | 59 | 4-162 | 8 | 94 | 6-165 | 5 |
| Early Summer | 36 | 1-275 | 50 | 45 | 1-279 | 40 |
| Late Summer | 63 | 1-201 | 12 | 75 | 3-208 | 11 |
| Early Fall | 64 | 1-233 | 22 | 88 | 2-342 | 16 |
| Late Fall | 13 | 2-20 | 7 | 13 | 2-20 | 7 |
| Entire Active Year* | 46 | 1-275 | 99 | 58 | 1-342 | 78 |

*Excludes the period in which the sow was immobilized.
+Excludes breaks in rest of less than 30 seconds.
++Excludes breaks resulting from nursing and excludes other types of breaks of 3 minutes or less.

## FEEDING/FORAGING ACTIVITY

### Classifications and Definitions

All activities in which a bear was actively engaged in feeding or in the immediate process of searching for food was classified as Feeding/Foraging (F/F). This category was subdivided as described below.

#### Nursing and Nursing Attempts

This classification was included in the F/F category for the young but not for the sow. Feeding percentages for the sow (Table 2) therefore do not include the time the sow spent nursing the cubs but feeding percentages for the cubs do include the time they spent nursing or attempting to nurse. Nursing is discussed separately in a later section.

#### Digging Roots

Feeding on or foraging for below-ground roots.

#### Grazing

Feeding on or foraging for above-ground vegetative material (either grazing or browsing).

#### Carcass

Actual feeding on animal foods, either killed by the bears or in the form of carrion.

Searching for Ground Squirrels

This classification involved foraging for ground squirrels, but did not include actually digging for them. For the sow this involved moving from one ground squirrel hole to another and sniffing out active burrows which might be profitably dug. For the cubs this involved searching holes previously dug by the sow for ground squirrels or ground squirrel scraps.

Digging Ground Squirrels

This classification involved actually digging out burrows in an attempt to catch and consume arctic ground squirrels.

Searching and Digging for Ground Squirrels

Mixture of searching for and digging ground squirrels which were not separated into one category or the other.

Watching the Digging of Ground Squirrels

This classification applied only to the cubs and involved actively watching and waiting as the sow or other cub dug for ground squirrels.

Predation

All chases (or stalking) of prey, whether successful or unsuccessful.

Searching

Pure foraging behavior, in which no feeding was involved, but in which an active search was clearly in progress for a particular but not

clearly ascertainable food source. Normally it involved a head down wandering search, sometimes with scenting of the wind.

Unknown

Mixtures of 2 or more feeding types which were undistinguishable or could not be separated as to begining and ending times of each due to distance, darkness, and/or vegetative cover.

## Results and Discussion

The 3 most important feeding classes over the year in terms of time spent in feeding/foraging activity were grazing, digging roots and ground squirrel hunting (both searching and digging). Grazing was the most common F/F activity for all family members and was followed more distantly by the other two major feeding activities. Ground squirrel hunting was a much more important activity for the sow than for either of the cubs. The proportion of time each bear was observed in various known feeding activities is tabulated in Table 5 and the proportion of unknown feeding activities in Table 6.

The proportion of time spent in any one F/F class varied widely from season to season. In the spring digging roots, in which plant nutrients were stored overwinter, dominated almost to the exclusion of all other types of F/F activities. Ground squirrels were not observed to be sought at this time, and only a few overwintered berries (Arcto-staphylos rubra) were available. A sharp transition from digging roots to grazing occurred beginning about 7 June and almost all of the spring

Table 5. Yearly and seasonal feeding activities of the family group (percent).

| | Nursing | Nursing Attempts | Digging Roots | Grazing | Carcass | Searching Ground Squirrels | Digging Ground Squirrels | Searching Digging Ground Squirrels | Watching Digging Ground Squirrels | Predation | Searching Unidentified Food Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sow | | | | | | | | | | | |
| Spring | - | - | 95.9 | 1.8 | - | - | - | - | - | 0.9 | 1.4 |
| Early Summer | - | - | 1.6 | 80.7 | 8.5 | 0.1 | 7.6 | - | - | 0.2 | 1.4 |
| Late Summer | - | - | - | 99.3 | - | - | 0.6 | - | - | 0.1 | - |
| Early Fall | - | - | 19.8 | 38.8 | - | 18.4 | 22.9 | - | - | 0.1 | - |
| Late Fall | - | - | - | 25.2 | - | 22.1 | 24.8 | 27.0 | - | - | 0.9 |
| Entire Active Year | - | - | 16.2 | 66.4 | 2.2 | 5.2 | 8.5 | 0.8 | - | 0.2 | 0.5 |
| Cub 1 | | | | | | | | | | | |
| Spring | 2.8 | 0.3 | 95.0 | 1.5 | - | - | - | - | - | 0.4 | - |
| Early Summer | 2.5 | 0.4 | 0.2 | 75.6 | 18.7 | 0.1 | 1.4 | - | 0.6 | 0.3 | - |
| Late Summer | 0.3 | - | - | 99.2 | - | 0.1 | - | - | 0.2 | 0.2 | - |
| Early Fall | 1.2 | 0.1 | 41.0 | 42.4 | 0.4 | 0.4 | 2.8 | - | 11.8 | 0.1 | - |
| Late Fall | - | - | 9.0 | 48.6 | - | - | 24.3 | - | 15.3 | - | 2.7 |
| Entire Active Year | 1.6 | 0.2 | 30.9 | 58.4 | 4.6 | 0.1 | 1.2 | - | 2.7 | 0.3 | 0.0 |
| Cub 2 | | | | | | | | | | | |
| Spring | 2.4 | - | 95.5 | 1.6 | - | - | - | - | - | 0.4 | - |
| Early Summer | 2.6 | 0.3 | - | 81.9 | 14.4 | 0.1 | - | - | 0.5 | 0.2 | - |
| Late Summer | 0.3 | - | - | 99.4 | - | 0.1 | - | - | 0.1 | 0.1 | - |
| Early Fall | 1.3 | 0.3 | 42.0 | 45.9 | - | 0.6 | - | - | 9.8 | 0.0 | - |
| Late Fall | - | - | - | 39.2 | - | - | 14.7 | - | 42.2 | 1.0 | 2.9 |
| Entire Active Year | 1.5 | 0.1 | 29.7 | 62.1 | 3.3 | 0.2 | 0.2 | - | 2.6 | 0.2 | 0.0 |

Table 6. Unknown feeding activity as a percentage of total observed feeding times.

| | Sow | Cub 1 | Cub 2 |
|---|---|---|---|
| Spring | 25.3 | 13.3 | 22.8 |
| Early Summer | 3.7 | 6.3 | 7.1 |
| Late Summer | 5.9 | - | - |
| Early Fall | 47.2 | 53.9 | 56.8 |
| Late Fall | 61.4 | 79.1 | 78.5 |
| Entire Active Year | 25.2 | 24.9 | 27.9 |

grazing activity observed for the family unit occurred during this transition period on 7 and 8 June. This transition period was associated with the emergence of new vegetation in early snow melt areas as plants started shifting nutrients from roots to shoots. A substantial amount of the family's feeding activity at this time involved mixed patterns of digging roots and grazing which could not be separated readily and which were classified as unknown.

In early summer most feeding activity was composed of grazing. Some feeding took place on caribou carcasses, and some feeding/foraging for ground squirrels took place, particularly by the sow. Bears spent very little time digging roots during early summer. What little digging did take place was almost entirely attributable to observations made on the first day of this season on 9 June. The transition stage during which roots were being consumed in rapidly diminishing quantities probably continued for 1 or 2 more days. By the next observation period on 15 June, time spent digging roots appeared to have become negligible.

In late summer grazing continued to be the most dominant feeding/foraging activity observed - even more so than during early summer. Caribou had left the area and were no longer available, ground squirrel burrows were dug less (probably due to heat and mosquito harassment) and roots were not observed to be utilized at all. Feeding activity for all family members was therefore almost entirely composed of grazing for the observed portion of late summer.

A dramatic shift again occurred in feeding activities during the early fall season. For the sow ground squirrel related feeding activity became codominant with grazing and digging roots again became an important

feeding activity. For the cubs time spent digging roots became just about equal to that spent grazing, and ground squirrel related feeding activities started to become an important part of their feeding behavior. During early fall grazing activity for both sow and cubs appeared to diminish steadily and then level off, possibly as a result of the dying off of above ground herbaceous vegetation now that the growing season had ended and the greater nutrient value of roots as plants shifted nutrients from above ground growth to below ground storage.

Limited data were obtained during late fall due to extensive bad weather which severely reduced observation time. Also as a result of bad weather, increasingly limited daylight hours, and distance, observations were not generally as sharp and detailed as during other seasons so feeding patterns were much less clear. Still, based on the limited data available, it appears that the late fall season feeding pattern was similar to that of early fall except perhaps that feeding/foraging on ground squirrels became proportionally even more important for the family unit than during the previous season, and digging roots less important. All family members were noted to dig roots, though to a lesser degree than in early fall, but incidents which were unclear in duration were classified as unknown and are not shown in Table 5. (Most of unknown feeding activites in early and late fall were undistinguishable mixtures of grazing, digging roots, and hunting ground squirrels.) Ground squirrel hunting appeared to be the single most important feeding activity of the sow during late fall and even the cubs spent a higher proportion of their feeding time trying (unsuccessfully) to dig out ground squirrels of their own.

Digging Roots

Vegetation Utilized. Roots dug by the family unit were identified as Hedysarum alpinum and Oxytropis borealis (Hechtel, 1979). Both are legumes which have nitrogen fixing bacteria associated with their roots and in addition to providing other stored nutrients may have been an important source of nitrogen in the spring.

Behavior. Several root-digging techniques were observed. When first observed in the spring the sow would stand in front of the plant and place both forepaws on the far end of the plant mat, hook her claws under and pull up, leaning back and using her body weight to do most of the work. The cubs dug roots the same way. The sow typically turned over the plant right away with little effort, while the much lighter, less powerful cubs often would have to pry and repeatedly rock back and forth to overturn it. On one occasion one of the cubs was noted to pull dirt away from the far end of the plant mat to create a groove in which to more deeply hook claws and paws. Late in spring, possibly due to deepening ground thaw levels, roots appeared to be extracted with greater ease by the sow and cubs and sometimes only a single forepaw was used to successfully overturn plants. Large areas were overturned by the family unit as they foraged for roots.

Once the root mat was overturned, roots were either eaten directly from the overturned mat or pulled loose from the mat and consumed. Frequently the cubs, who were less able to overturn the entire root structure, would dig out and consume roots remaining in the exposed hole as well. Dirt clots were cleaned from the roots with claws. The sow was substantially quicker and more efficient at extracting and consuming

roots than either of her yearlings. The male cub, cub 1, appeared to pursue this food source much more actively and successfully and consumed much more than the female, cub 2. Cub 2 tended to putter around inefficiently, dug roots much less, and often nibbled at roots rather than speedily consuming them. Frequently, cub 2 would lie down while slowly nibbling on roots, in a position much like that of a dog chewing a bone. Cub 2 seemed to prefer whenever possible to extract leftovers from root mats already overturned by the sow or cub 1, and thus minimize her own energy expenditure. Cub 2 appeared to be in poor condition when observed during the spring season and this may have affected her feeding behavior at this time, especially since digging roots probably required a relatively large expenditure of energy during most of the spring season. Cub 2 was slightly smaller than cub 1 and weighed only 14 kg. This was the lowest weight recorded among 6 yearlings weighed by Reynolds (1980) in the study area. Weights of the other yearlings were 22, 26, 26, 34, and 41 kg, respectively. One especially large cub of the year, whose weight was recorded within a week of cub 2 weighed 17 kg.

## Grazing

Vegetation Utilized. Plants known to be grazed by the family unit included Equisetum arvense, Boykinia richardsonii (leaves, stems and flowers), Oxytropis borealis (flowers), Arctostaphylos rubra (berries) and various grasses and sedges (Hechtel, 1979). New growth herbaceous material, and later, flowering parts, appeared to be the predominant material selected in early summer. In late summer the tops of grasses and sedges seemed predominant. In early fall and late fall berries were the predominant grazing material.

Behavior. Family members would move from plant to plant and either stop and feed, stop and take a bite and continue moving, or take a bite while moving. Typically when grazing the tops of the plants were bitten off. Arctostaphylos berries, which were scattered over the plant, tended to be nibbled off selectively; sometimes forepaws were used to assist.

During the period of observation in late summer the time spent actually feeding while grazing, as opposed to foraging, appeared much lower than during other seasons. This may well have been a result of mosquito harassment forcing the sow to keep moving almost constantly and preventing her from stopping for long to feed.

## Ground Squirrel Hunting

Ground Squirrels - General. The arctic ground squirrel hibernates from October until about the beginning of May in northwestern Alaska, breeds during mid-May, and has litters during the first half of June. The young are driven from the natal burrow during August and establish their own solitary territories by mid-September. Perennial burrows are located in well drained sites in creek banks, hillsides, and raised mounds of porous material in flat tundra - all of which have a comparatively deep permafrost level. Refugee populations tend to occupy less favorable sites with shallower burrows and are subject to heavier mortalities in general and predation mortalities in particular (Carl, 1971).

Yearly and Seasonal Percentages - Sow. The sow spent 14.5% of her total feeding time over the year hunting (both searching for and digging out) ground squirrels. Searching for ground squirrels made up over 5%

of total feeding/foraging activity and digging for ground squirrels about 9%.

Seasonally the time spent in searching and digging activity was greatest in the fall. In the spring, the sow was not observed to hunt ground squirrels (although it is not uncommon for grizzlies to do so). In early summer, time spent searching for ground squirrels was negligible, but time spent digging for ground squirrels made up about 8% of total feeding activity. In late summer searching for ground squirrels became more important but occurred along with grazing activity. Such indistinguishably mixed grazing/searching for ground squirrel activity was classified with unknown behaviors. Digging for ground squirrels was substantially reduced in late summer, probably due to high temperatures and mosquito harassment. In the early fall ground squirrels became much more important in the sow's diet; searching for ground squirrels made up about 18% and digging ground squirrels 23% of her feeding activity. In late fall searching and digging increased to even higher levels and together made up about 75% of the sow's total feeding activity. Late fall percentages are questionable to some extent, due to the limited observations during this season.

Fall Increase in Utilization. According to observations made by Carl (1971) on the northwestern coast of Alaska, only beginning in early August (the beginning of early fall season in this study) did the widespread perennial burrows with their relatively deep permafrost levels, thaw sufficiently to make their deepest reaches readily accessible to bears. (Data from Umiat [U.S.D.I., 1978a] suggests ground thaw in the study area continues through the end of August.) Refugee squirrel

burrows, which appeared to be more susceptable to predation, were also being established during August. Weight and caloric value of adult ground squirrels have nearly reached their highest value by the beginning of August and weights of the young are increasing dramatically. Beginning at about this time, shortly after the start of early fall, ground squirrel related searching and digging activities by the sow increased dramatically and ground squirrels became an important food source for the family.

A similar seasonal pattern of sporadic hunting for ground squirrels followed by a large fall increase in ground squirrel hunting activity was reported by Murie (1981) and Stelmock (1981) in Denali National Park, Alaska. The percent time spent hunting ground squirrels in the fall in my study, however, appeared to be greater than that tabulated by Stelmock (1981). Perhaps accentuating the high fall ground squirrel hunting activity (both searching and digging) may have been the greater effort required to obtain berries for fall fat deposition in the study area compared with Denali Park. In the sow's home range the only widespread abundant berry utilized was Arctostaphylos rubra, whose single berries are widely scattered over the plant. In contrast, in Denali Park a variety of abundant edible berries are available in a concentrated clustered form. While often requiring a substantial initial effort to obtain, ground squirrels are a concentrated, digestible, nutritious, high calorie food and may be used more extensively in the study area to compensate for the areas relative deficiency of easily obtained berries. Ground squirrels are of particularly high caloric value in the fall when their fat reserves are highest.

An estimate of caloric value can be obtained if percentages of body fat and protein found in ground squirrels in the fall by Galster and Morrison (1976) and fall body weights recorded for ground squirrels on the North Slope of Alaska by Mayer and Roche (1954) are used to calculate energy values per ground squirrel (using 9 kcal/g of fat and 4 kcal/g of protein). I calculate the average energy value per ground squirrel to be roughly 3830 kcal/adult ground squirrel during the fall.

While some work is required to dig out a ground squirrel the energy expenditure is not great. Estimating the sow's basal metabolic rate using BMR = $70W^{.75}$ kg (Klieber, 1961) and using the sow's weight at the beginning of early fall (120 kg) and dividing by 1440 (minutes in 24 hours) a BMR of 1.76 kcal/min is obtained. Assuming that digging ground squirrels is comparable to heavy work for humans and further assuming that the ratio of metabolic rate while engaged in heavy work to basal metabolic rate is similar in bears and humans, an estimate can be obtained (based on a ratio derived from Durnin and Passmore [1967], cited by Lloyd et al. [1978]) of energy expended in digging ground squirrels. Using these assumptions an expenditure of 14 kcal/min is obtained. Using the average time the sow spent digging each burrow and her success rate (see following sections) an average energy expenditure of 350 kcal was found for each ground squirrel consumed and the net input per ground squirrel was 3480 kcal. (If time spent walking around and searching for ground squirrels in early fall and late fall is calculated and if BMR is assumed to double during this movement, an estimated 630 and 1130 kcal/day respectively was spent by the sow in search of ground squirrels.)

Frequency of Digging. At least 66 ground squirrel holes were observed to be dug by the sow over the year, with an average time per hole of about 10 minutes and a range of from 1 to 72 minutes. Based on the number of holes observed to be dug during each season and the total time directly observed per season, the frequency with which holes were dug per day was calculated. In the spring, no ground squirrel holes were dug, in early summer 3.00 per day, in late summer 0.27 per day, in early fall 13.55 per day, and in late fall 15.27 per day. This works out to be about zero holes in spring, 90.0 holes in early summer, 8.4 in late summer, 420.1 in early fall, 473.4 in late fall and roughly 992 holes over the entire active year (with a 95% Confidence Interval range of from 417 to 1575 holes). The assumption is made here that the digging rate for each season is equal to that occurring during observations made in each season.

Success Rate. The success rate for obtaining one or more ground squirrels when the sow dug out a hole was difficult to determine even under relatively ideal conditions. Frequently distance, darkness, vegetation and/or terrain hindered detailed observations. When they did not the sow often still obscured herself by digging a gaping hole in the ground in which she immersed her head and forequarters and occasionally, most of her body. The sow typically appeared to eat ground squirrels in the hole to block access by the cubs (and prevent them from stealing her prize) and to help prevent ground squirrels from escaping past her; thus only on those occasions when the sow emerged wolfing down the last bite(s), or a ground squirrel attempted to escape and was caught outside the hole, could success be clearly ascertained. Only 4 such clear

successes were observed. Three other probable successes were noted, based on behavior in which the sow remained immobile in the hole for a prolonged period of time and was strongly suggestive of a squirrel being consumed in the hole. Clear successes averaged 15.5 minutes and ranged from 4 to 26 minutes. Probable successes averaged 14 minutes (7, 17, and 18 minutes). Seven apparent failures also were identified. They averaged about 9 minutes and ranged from 2 to 17 minutes. Success rate based on these limited data suggest a minumum of 29% and a more probable maximum of 50% success. Usually only one hole was dug per burrow by the sow. More than one ground squirrel, however, may have been obtained in each hole or burrow during summer prior to the breakup of ground squirrel families.

Comparing success rates determined here with those in the literature is difficult because of the variety of methods of determining success which are not entirely comparable. Carl (1971) in his study area on the northwestern coast of Alaska, established a fairly accurate capture rate of 56% of all ground squirrels occupying attacked burrows in the fall by comparing known burrow populations before and after being dug by grizzlies. Murie (1981) based on extensive but untabulated observations, considered grizzlies in Denali National Park to be mostly successful in digging out and capturing ground squirrels. Pearson (1975), in contrast, considered grizzlies studied in a rugged area of the southern Yukon seldom to be successful at capturing ground squirrels until snow cover in late September made escape by ground squirrels more difficult. The extent of Pearson's (1975) observations was unclear and his very low success rate may have been due mainly to the difficulty of observing

'in-burrow' captures. The sow in my study also appeared to have poor success in capturing escaped ground squirrels but appeared reasonably successful in capturing them in their burrow where most such captures would normally be missed by an observer. Possibly terrain differences could play a role in determining success of different grizzly population but this seems doubtful since a grizzly is quite capable of digging almost anywhere a ground squirrel can burrow once ground thaw permits (unless for instance the burrow runs among large boulders). Variations in success between populations may be dependent on the learning of successful capture techniques or the extensiveness of the burrows and availability of escape holes built by the ground squirrel populations in the area.

Importance. Banfield (1958; 1964) considered ground squirrels highly important to barren-ground grizzly bears in northern Canada and states, "It is probable that bears could not live where ground squirrels are absent." He bases this largely on the similar distributions of arctic ground squirrels and barren-ground grizzlies in northern Canada though he does note that some interior grizzlies do appear to occupy range devoid of ground squirrels. He also suggests a similar relationship exists in the distribution of these two species in North America as a whole. It is probable, however, that the importance of ground squirrels to grizzly populations varies substantially from one area to another depending on their availability and the availability of alternative foods. Grizzly bears are highly opportunistic in their feeding and may commonly utilize such alternative foods as fish, various other rodents, nesting birds, insects, and carrion.

Other authors, however, have suggested that ground squirrels are typically only a minor food item in a northern grizzly's diet, even in the fall (Murie, 1944; Dean 1957; Reynolds, 1976). Murie (1981), however, in a later paper, after much more intensive observations of grizzlies, does note that ground squirrels were hunted systematically in the fall and with considerable success. Dean (1957) considered ground squirrels to be unimportant to grizzlies because he believed the expenditure in capturing ground squirrels to almost invariably be greater than their worth to the bear. Stelmock (1981) suggested that energy expenditures were probably very great, but believed they are sought anyway as a necessary source of protein. No one, however, has made more than a cursory examination of their importance.

In my study, ground squirrels were found to be highly important and estimates of energy expenditure in digging for them suggests this cost is minor compared to the caloric value they provide. If it is conservatively assumed that one adult ground squirrel occupied each hole dug by the sow, and using the mid-range success rate of 40%, the sow would have captured and consumed some 397 ground squirrels over the entire active year with a seasonal intake of roughly 0 in the spring, 36 in early summer, 3 in late summer, 168 in early fall and 189 in late fall. Using seasonal weights of arctic ground squirrels reported by Mayer and Roche (1954) yearly consumption of ground squirrels would amount to 358.5 kg (790.5 lb). Seasonal consumption accordingly would be 0.0 kg in the spring, 23.7 kg (52.3 lb) in early summer, 2.6 kg (5.7 lb) in late summer, 155.4 kg (342.7 lb) in early fall and 176.8 kg (389.8 lb) in late fall. Thus, ground squirrel hunting activity, while involving some

effort, pays off in quite substantial returns of meat for the sow's diet.

These are ball park estimates since it is assumed that only 1 squirrel occupied each burrow and it is assumed to be an adult. More than 1 ground squirrel certainly occupied some of the burrows prior to family break-up during August, since average litter size of females is 7.8 young (Mayer and Roche, 1954) and in the fall, sole occupants of burrows were not necessarily adults. Weight of the young is about 84% of adult weight in mid-early fall and 96% in mid-late fall (based on data from Mayer and Roche, 1954).

Quantities consumed in early fall and late fall are equivalent in weight to nearly 2 average adult female caribou per season, and are probably considerably higher in fat content and caloric value. As noted earlier each ground squirrel has a caloric value of about 3830 kcal during early and late fall. Seasonal consumption on a per day basis provided an average of about 0.79 kg (1.7 lb) of meat per day in early summer, about 0.08 kg (0.2 lb) per day in late summer, about 5.01 kg (11.1 lb) per day in early fall and about 5.70 kg (12.6 lb) in late fall.

Based on the data above, the caloric intake from ground squirrels alone provided a daily average intake of about 20,800 kcal in early fall and 23,400 kcal in late fall (18,900 and 21,300 kcal respectively if energy expended digging them out is subtracted from this and 18,200 and 20,100 kcal respectively if energy expended in searching for them is also subtracted). Caloric estimates from late fall while very similar to those of early fall are, however, as noted previously, based on a

much smaller sample size. If raw data from the similar early fall and late fall seasons are combined more precise confidence limits can be placed on overall caloric intake from ground squirrels in the fall. Caloric values from ground squirrels in the combined fall seasons are found to be 21,100 kcal/day with 95% Confidence Interval of between 13,500 and 28,600 kcal/day.

The success rate in catching ground squirrels plays an important role in determining daily caloric value from ground squirrels. If instead of the mid-point, the minimum success rate of 29%, mentioned previously is used, average fall intake would be about 15,300 kcal/day (with a 95% C.I. of 9800 to 20,800) and if the higher percentage of 50% (which included highly likely successes) is used, it would be about 26,300 kcal/day (with a 95% C.I. of 16,900 to 35,800). Based even on the most conservative of these estimates, the importance of ground squirrel hunting activity to the sow appears to be considerable.

Ground squirrels, which are rich both in protein and minerals, may also be especially valuable to the sow as a lactating mother, since she may have depleted much of her own protein and mineral reserves in nursing and may well need to build surpluses for resumption of nursing at normal levels the following spring.

Yearly and Seasonal Percentages - Cubs. Dramatic differences existed between the sow and her yearlings in terms of ground squirrel foraging activity. The cubs spent considerably less time then the sow engaged in searching activity, with searching making up 0.1% and 0.2% of the cubs' feeding activity over the year compared with about 5% for the sow. Searching for ground squirrels by the cubs consisted entirely of

checking holes previously examined or dug by the sow or the other cub, or checking holes adjacent to the one being dug by the sow. No systematic search for ground squirrels such as was performed by the sow was observed for the cubs.

Time spent digging ground squirrels was also considerably less for the yearlings compared to the sow, and strong differences were also observed between the cubs in digging activity. Cub 1 spent 1.2% of his feeding time over the year digging ground squirrels while cub 2 spent only 0.2% of her time digging ground squirrels - a 6-fold difference. Cub 1's attempts to dig ground squirrels stretched sporadically from early summer through late fall, reaching highest levels in late fall. Cub 2's attempts consisted of a single sporadic, perhaps imitative attempt in late fall in which she dug along with cub 1. Cub 1's attempts, while enthusiastic, were never observed to be successful due to his much smaller size and lack of strength compared to an adult bear. Cub 2 appeared well behind cub 1 in the development of behavioral patterns related to digging for ground squirrels.

Considerable strength is required to successfully dig out ground squirrels, or for that matter, to dig out a den to survive the winter on the North Slope. The ability to dig ground squirrels is probably a strong measure of a young bear's maturity and of their ability and readiness to survive on their own without maternal support. Neither yearling appeared close to the point where it could survive on its own in the harsh environment of the North Slope. It did not appear likely that cub 1 could reach this point for at least another year and cub 2 for another 2 years. It is not surprising, considering the harsh condi-

tions, the short active season, and the correspondingly slow development of the young, that grizzly females on the North Slope typically do not wean their young until they are 3-years old and a few not until the spring as 4-year olds (Reynolds, 1980).

Besides searching and digging for ground squirrels the cubs also spent time watching the sow dig, or sometimes cub 2 would watch cub 1 dig. This was the type of ground squirrel related activity the cubs were involved with most: waiting and watching and ready to catch a squirrel. Both cubs spent roughly equal times in this activity; cub 1, 2.7% of yearly feeding activity and cub 2, 2.6%. As with other ground squirrel related activities, most took place in the fall.

Ground squirrel related activities of all types made up 4% of cub 1's and 3% of cub 2's yearly feeding activity. Seasonally cub 1's ground squirrel related activity made up 0.0% of feeding activity in the spring, 2.1% in early summer, 0.3% in late summer, 15.0% in early fall and 39.6% in late fall. Seasonally cub 2's ground squirrel related activity made up 0.0% of feeding activity in the spring, 0.6% of feeding activity in early summer, 0.2% in late summer, 10.4% in early fall and 56.9% in late fall. Late fall values are questionable due to the small sample size.

Behavior. In searching for ground squirrels the sow would typically move from one burrow to the next and sniff around at one or more holes to determine if they were promising. She then would begin either to dig at one of the holes or move on to an adjacent burrow and repeat the process. If no other burrows were near she would generally move to another area and locate a burrow and repeat the process. The sow appeared

to have no trouble locating burrow areas, and upon arrival, locating individual holes and determining occupancy. Possibly the sow was able to locate burrows through past familiarity with her home range and/or possibly through an ability to recognize readily types of areas utilized by ground squirrels for burrows and through her keen sense of smell.

When digging for ground squirrels the sow would use either one or both forepaws simultaneously and shovel rocks and dirt behind her in a spray - much like a dog digging a hole. Larger rocks were pulled out using both forepaws. Sometimes the sow would give up after a short time when she apparently decided the effort unprofitable. At other times she would continue digging vigorously for as long as well over an hour. Sometimes she would become almost totally hidden by the hole she was digging. Such huge holes were dug as early as 9 June in favorable spots. These huge holes could require as little as 16 minutes or as long as 72 minutes to dig. While digging the sow would sometimes periodically pause in her digging to sniff at the hole, apparently gauging how close she was to the ground squirrel or deciding which branch of the tunnel to dig. Sometimes a ground squirrel(s) would make a break to escape and the sow would chase it - usually without success (see Predation).

Frequently, the cubs would watch the sow as she dug for ground squirrels, waiting to catch any ground squirrels which might rush from a hole and try to escape, and perhaps learning from watching the sow. The cub's success in catching escaping ground squirrels was variable. Often the cubs would rest by the sow as she dug, until they became aware (possibly through some vocalization by the trapped squirrel or by an

excited or agitated sow) that the sow was getting close or was successful, and then they would become very attentive and sometimes try to crowd in on either side of the sow. In one instance a fight was observed to ensue between the cubs as a result. On another occasion, cub 1 stole a ground squirrel the sow had just caught. Typically the sow used her body to block access to the hole by the cubs and to help prevent ground squirrels from escaping past her. Occasionally the sow's endeavors seemed to inspire cub 1 to try his hand at extracting ground squirrels and he would dig vigorously at an adjacent hole scattering dirt widely but making only a slight depression in the ground. When the sow abandoned a ground squirrel hole the cubs often would check it out, sniffing around the hole presumably for any missed scraps if the sow was successful. Occasionally cub 1 would begin digging at a hole abandoned by the sow. A threat and several fights were observed between the cubs over access to holes abandoned by the sow.

Predation

Predation as used here refers to the approach or chasing of prey species by the bear(s) in an attempt to capture and consume it. Digging for ground squirrels is treated separately in the previous section. Attempts by the sow and cubs to capture escaping ground squirrels are, however, discussed herein. Predation was a relatively minor activity in terms of time spent and made up well under 1% of the sow and cubs' feeding activity during all seasons of the year.

Ground Squirrel - Sow. Twelve ground squirrels from 7 different burrows were observed to attempt to escape as the sow dug out their

burrows. All appeared to run from the hole she was digging but some may have run from adjacent holes in the burrow. Nine of the 12 were chased by the sow, 5 without success, 2 with unknown success (having chased them into areas obscured from view), 1 questionably and 1 successfully. The 5 failures were observed at 1 hole in late June where 2 squirrels escaped followed by 3 single escapes. Typically when a ground squirrel got past the sow, the sow would turn, lunge at it, miss it, chase it again and pounce at it. This sometimes occurred several times with repeated chasing and pouncing, but always missing - though often narrowly. The ground squirrels were amazingly fast and agile despite their short legs. The chase was usually very short with the ground squirrels finding another hole in short order. While the sow undoubtedly caught some ground squirrels in the chase, her success in capturing them in this manner was poor. The sow's forte appeared to be catching them bottled up in their burrows and perhaps as they tried to escape past her. In the incident of questionable success the sow may have gotten the squirrel on her first wild lunge, or perhaps one of the cubs waiting behind her did. In any case, the sow lost the ground squirrel to cub 1 in the juggling tug of war that ensued among all 3 family members over the ground squirrel. In the single successful capture outside the hole the ground squirrel appeared to try to slip through the sow's legs and the sow was observed to backpeddle out of the hole rapidly, trying to catch and pounce on it with her forepaws. She succeeded in so doing on the periphery of her excavation. (Just as she was about to consume it, however, cub 1 slipped around her, snatched it from her and ran off with it.) Of the instances where the sow did not bother to chase the fleeing

ground squirrels, in 1 instance a group of ground squirrels appeared to flee simultaneously from the hole the sow was digging. Two got by her, apparently either around her or between her legs. One (possibly more) was captured by the sow as it tried to get past her and was consumed in the hole (where she successfully blocked cub 1 in his attempt to gain access to it). The sow's immediate preoccupation with consuming the ground squirrel and/or with protecting it from the cubs, apparently prevented her from abandoning her kill temporarily to attempt to capture the other escaping squirrels. In the other instance a single ground squirrel escaped and the sow remained at the hole. It is not known whether she had caught another ground squirrel and was consuming it or had missed its escape, possibly from an adjacent hole.

Two instances were observed, in late August, in which a single ground squirrel appeared either to be caught foraging away from its burrow or was a refugee temporarily without a burrow, and was chased unsuccessfully by the sow and cubs before escaping to a hole in the area. All in all the sow had poor success in capturing ground squirrels outside their burrows prior to heavy snow accumulation in late fall.

Ground Squirrels - Cubs. The cubs were observed at 6 different burrows at times when ground squirrels were observed to attempt escapes. In 1 instance, 2 ground squirrels escaped and, as noted, the sow remained busy at the hole with a third. Each ground squirrel ran in a different direction and was chased by a cub. Cub 2's squirrel ran right past her and she was successful in capturing it. Cub 1, however, was unsuccessful and approached both cub 2 and the sow in an apparent attempt to steal theirs. In another instance, 1 ground squirrel got past the

sow, the sow turned and lunged at it, as did both cubs, and a wild melee ensued in which the ground squirrel was juggled in the air between all three bears and cub 1 finally came up with the squirrel. In a third instance, 1 ground squirrel escaped and was unsuccessfully pursued by cub 1. In a fourth case, the sow caught an escaping ground squirrel on the periphery of the dig, as noted above, but cub 1 stole it from her. In 2 other instances, a single ground squirrel escaped and both cubs joined the sow in the chase, with unknown results due to their moving out of view. One other incident was noted in which one of the cubs was first observed at the start of daily observations in the process of consuming a ground squirrel it had just obtained in some unknown manner. As noted, 2 other instances were observed in which a ground squirrel was found outside of a burrow and was unsuccessfully chased by the entire family.

In all, cub 1 was involved in 7 predation attempts, 4 unsuccessful, 2 unknown and 1 questionable. Cub 2 was involved in 6 predation attempts, 2 unsuccessful, 1 successful, 2 unknown and 1 questionable. In all the cubs consumed 4 ground squirrels while observed; only 1 clearly through predation by cub 2; 1 stolen by cub 1 from the sow; 1 in which it was uncertain which bear first caught it (though probably the sow) but which cub 1 obtained; and a fourth in which one cub (which one is unknown) obtained a ground squirrel through unknown means.

If the limited directly observed seasonal successes in obtaining ground squirrels through whatever means is projected over each season, we find that no ground squirrels were consumed by the 2 cubs in spring, 9.1 in early summer, 0.0 in late summer, 17.5 in early fall and 67.6 in

late fall for a total of 92 ground squirrels over the year. Considering the very limited data on which the projections are based they should be viewed as speculative in nature. It is unclear whether the extremely high number projected for late fall is a result of the much smaller observation time in late fall (compared with other seasons) providing an anomalous sample of that period or whether it might reflect a heavy snow cover making those ground squirrels escaping past the sow easy prey for the waiting cubs. If it is conservatively assumed that late fall success was only half as great as projected (33.8), a total of about 60 ground squirrels still was consumed over the year between the 2 cubs. Using seasonal weights of ground squirrel obtained from Mayer and Roche (1954) seasonal consumption is about 6.0 kg (13.2 lb) in early summer, 16.2 kg (35.7 lb) in early fall and 31.6 (69.6 lb) in late fall. Assuming arbitrarily that each cub obtained an equal share, this breaks down to 0.10 kg (0.2 lb) per cub per day in early summer, 0.26 kg (0.6 lb) per cub per day in early fall and 0.51 kg (1.1 lb) per cub per day in late fall. Early fall caloric consumption from ground squirrels would then be 1000 kcal per cub per day and in late fall 1950 kg per cub per day. Sample sizes are too small to provide reliable estimates of the proportion of ground squirrels obtained by each cub but based on cub 1's success in 2 out of 3 of these known instances, largely as a result of taking them away from other family members, and based on cub 1's overall aggressiveness in regards to feeding activity, it seems likely that cub 1's share of ground squirrels was actually greater than cub 2's.

Another female grizzly was also observed during the early fall season. This female had 2 cubs of the year as opposed to the primary

subject of this study who had 2 yearlings. The female with spring cubs was observed to dig ground squirrels for a time and was watched closely by her cubs. After this female had dug at a hole for about 4 minutes, the ground squirrel made a break and escaped. The female and both spring cubs followed in hot pursuit. After about 20 seconds, the sow caught the ground squirrel and both cubs immediately rushed in trying to grab it from her. One of the cubs was successful and immediately ran off with it. It then ran around with the ground squirrel in its mouth. The sow showed no aggression and only made 1 attempt to regain it - when the cub ran near her again she started to rush toward it and the cub ran off again and finally stopped and consumed it.

Predation of escaping ground squirrels is probably more difficult for spring cubs than for yearlings. The spring cubs observed were even more clearly incapable of digging out their own ground squirrels than were the yearlings in this study. It is likely that stealing, largely from the sow, is the easiest and probably the most important method by which spring cubs and yearlings obtain ground squirrels during the year, with the possible exception of late fall when snow cover may render escaping ground squirrels susceptible to capture by the cubs.

If projections of the numbers of ground squirrels obtained by the yearlings in this study are even the crudest approximation of actual numbers obtained by grizzly cubs in general in the study area, it suggests ground squirrels may be an important supplemental food source for the cubs in the fall.

Caribou. The sow's home range lies on the periphery of the calving ground for the Western Arctic caribou herd where calving occurs between

the end of May and early June. The sow payed unusual attention to caribou herds at this time and was observed to make several predation attempts on caribou during or shortly after the calving season. She had only one success, a calf whose mother had died in the vicinity of the bear family.

The first predation attempt was observed on 8 June. Two adult and 1 yearling caribou were observed traveling and feeding in a westerly direction and their movements carried them directly upwind of the feeding sow and cubs. A low ridge between them hid each group from the other. As soon as the sow caught scent of the caribou, she immediately ran in their direction. The sow appeared to lose the scent when she reached the lee side of the base of the ridge. She then started wandering back and forth along the ridge base trying unsuccessfully to pick up the scent again before finally starting up the ridge. As she moved up the ridge, she again caught the scent and began to stalk them with her cubs following. When she got within roughly 50 m (150 ft) of the closest caribou, it spotted her and started to run. The sow chased them for about 275 m (900 ft) before giving up. The sow never came close to the caribou, but afterward she appeared quite agitated. She walked rapidly for another 150 m (500 ft), stopping every 30 m (100 ft) or so to dig or graze a bit, and then defecated. The incident lasted approximately 10 minutes. Surprisingly, on the next day, 9 June, a number of caribou passed within 8 m (25 ft) of the resting sow and cubs, feeding along apparently unaware of the bears. The sow, though she frequently looked up and must have been aware of them, appeared uninterested.

A more indirect predation attempt was observed on 15 June. A caribou herd was feeding nearby and the sow stopped her feeding and looked around and watched the herd. The sow with her cubs then travelled downwind of the herd and began grazing about 90 m (300 ft) away. After 4 minutes, the sow again began traveling with her cubs directly toward the caribou herd. The caribcu repeatedly moved away a little and the sow continued walking fast toward them with her cubs running and walking behind trying to keep up with her. Finally since the caribou invariably continued to move away as she tried to move closer, the sow gave up and resumed grazing. The sow appeared to have tried to maneuver herself within striking distance of the herd without alarming them by charging. (Unknown to the sow a crippled caribou was available only 150 m [500 ft] from her original position.)

The single successful predation incident began at 2043 h on 15 June and culminated several hours later at 0009 h on 16 June. The ultimate success was preceded by numerous failed attempts by family members. At 2043 h the sow was observed to repeatedly scent the wind as though she vaguely detected something of interest. Finally she appeared to catch a clear scent of something and began to run toward it with her cubs. Shortly they shifted to a walk, but when about 50 m (150 ft) away, again shifted to a run. When about 8 m (25 ft) away, a caribou calf sprang up from the carcass of its dead or dying mother and ran off with the grizzly family in pursuit. The calf maintained a continuous lead over the sow throughout the chase. During the chase, the cubs repeatedly looked back at the carcass and the sow halted twice in her chase to stop and look back. Finally all 3 gave up and returned to the dead cow, sniffing

around the area for a minute before beginning to feed at 2047 h. The calf halted about 180 to 210 m (600 to 700 ft) away.

At 2052 h, the sow stopped feeding and walked around for a minute and a half, checking the wind - possibly for another bear in the area - before resuming feeding. At 2112 h, the sow stopped feeding and began covering the carcass. Not long after the calf started moving very gradually back to the cow and was chased again by the sow and cubs at 2124 h. After running perhaps 50 m (150 ft), the bear family stopped and so did the calf. The sow then dug around a bit and walked back to the carcass. She then resumed covering the carcass while the cubs rested by it.

At 2150 h, cub 2 resumed feeding on the carcass and the calf meanwhile approached to 75 m (250 ft) and then shortly retreated again to about 150 m (500 ft) - apparently unnoticed by the bears. At 2207 h, the sow resumed feeding on the cow and finally rested at 2240 h. At 2243 h, cub 1 started moving toward the calf and the calf in turn started moving toward cub 1. When the two approached to within 3 m (10 ft) of each other, cub 1 started to run at the calf and the calf turned and ran. Cub 1 chased the calf about 4 to 5 seconds, stopped and dug a little and the calf moved almost directly between cub 1 and the resting sow and cub 2. At 2245 h, cub 1 rested by the sow and cub 2. At 2250 h, the cubs again resumed feeding on the caribou cow. The sow, while continuing to rest, raised her head periodically to check on things. The calf meanwhile kept trotting around getting as close as within 5 to 6 m (15 to 20 ft) of the bears. At 2253 h, and 2255 h, cub 2 and cub 1 respectively rested. The calf kept running back and forth nearby getting

bolder and bolder and finally approached to within 2 m (5 ft) of the sow, at 2309 h. The sow turned, looked, jumped up and pursued the calf, followed closely by the cubs. All 3 then stopped, continued watching the calf a moment more and turned and went back to the carcass. The sow and cub 2 then rested again while cub 1 resumed feeding.

At 2314 h the calf approached to within about 300 m (100 ft) of the bears, lay down for about 12 minutes, got up again, stood looking in the direction of the dead cow and bears, and then at 2330 h again approached close to the bears and the remains of the cow. Cub 1 again made an unsuccessful dash at it and the calf ran off. Cub 1 then rested by the sow and cub 2 (who were about 3 m from the carcass). Six minutes later the calf approached again, this time within 2 m (5 ft) of the covered-over carcass. Cub 1 sprang up and again chased the calf for a couple seconds and then fed some more on the carcass. Cub 2 joined him 2 minutes later. At 2345 h, cub 2 rested again by the sow and at 2350 h, the calf approached yet again, this time to within about 2 m (5 ft) of the resting sow and cub 2. Cub 2 lunged at the calf and again the calf ran off. At 2352 h, the calf again approached the resting sow and cub 2, to within about 2 m (7 ft), and cub 1 this time ran from the carcass to chase the calf, stopping at the sow and cub 2 as the calf ran off. At 2352 h, the sow nursed the cubs for 4 minutes and then all got up and shortly thereafter, began feeding on the carcass. At 0003 h on 16 June, cub 1 moved 3 m (10 ft) off and rested, and a minute later the calf walked over to him. Cub 1 sprang up, leaped about 2 m (5 ft) at the calf and stopped. The calf ran off about 10 m (30 ft) and then moved away at a walk. Cub 1 then resumed feeding at the carcass and the calf

walked back and lay down about 6 m (20 ft) from the feeding bears.

Finally at 0009 h, the sow began walking slowly toward the resting calf, stopping twice for about 10 second intervals. Cub 1 followed off to one side. When the sow got within 1 m (2 to 3 ft), the calf jumped up and the sow on her second bound grabbed the calf in her mouth, biting it on the back at the base of the neck and smashing it on the top of the back just foward of the hind quarters with her right front paw. Almost immediately, the sow swung around, running with the calf carried in her mouth and cub 1 beside her, and brought it back to the remains of the cow. All 3 bears then proceeded to consume the calf.

When first observed, the adult cow caribou was lying on her side and appeared to be untouched until discovered by the bears. The cow probably had died recently or was dying. The calf was probably about a week old, appeared to be in good condition and was quite capable of outrunning the sow. It is doubtful that the calf could have survived on its own.

The calf probably was drawn back repeatedly to the carcass area by the smell of its mother rather than by visual cues since by the time the calf was finally killed, little of its mother's carcass appeared to remain. Despite repeated chases by the bears, the calf gradually appeared to lose much of its fear of them and returned at shorter and shorter intervals, retreated shorter and shorter distances, and finally even bedded down nearby.

In this encounter, the sow made 3 unsuccessful attempts in which both cubs participated, cub 1 made 5 unsuccessful attempts on his own and cub 2 made 1 unsuccessful attempt on her own before the sow was finally successful.

Miscellaneous. Several other miscellaneous species were chased by the bears over the year and are noted below in order of date of occurrence.

On 14 July, the sow and cubs were observed crossing through the willows along a creek. Several minutes later the sow emerged chasing an unidentified fairly large white bird which was either injured or performing a 'broken wing act', to draw the sow from her brood. Several minutes later, the cubs were observed chasing white birds and continued to do so for several minutes. Success was unknown, but considering the large number of nesting birds in the area, it is likely that birds and possibly eggs played a role in their diet.

On 16 August, cub 1 appeared to have scented something and repeatedly sniffed the air. He then moved toward the scent (followed by cub 2) and appeared to pounce on and gobble down a small animal - possibly a vole or small bird.

Encounters between family members and a golden eagle and ravens were observed, but the intent of the bears was difficult to interpret. On 3 September, a golden eagle was observed making low passes over the sow while she dug for ground squirrels, perhaps hoping to benefit from the sow's work. The eagle then landed on top of a dirt covered hill overlooking the sow's digging. When the sow finished, she walked up the hill toward the eagle who flew off when she approached to within 15 to 25 m (50 to 75 ft). Since the sow resumed digging for ground squirrels in a hole in this direction shortly thereafter, her approach may have been intended to scare the eagle off, a predation attempt, or coincidental in nature.

On 22 September, another questionable incident was observed when, after the family scared off a pair of ravens, sniffed around the area and walked off, cub 2 continued to follow the ravens. The ravens repeatedly landed nearby, flew as cub 2 approached and landed a little further away. It is uncertain whether cub 2 was interested in the ravens as food or in some food scrap they may have had in their possession. Cub 2 gave up after about a minute.

Carcass

Yearly and Seasonal Percentages. Carcass feeding is used here to denote any observed time spent in the actual comsumption of meat. The sow spent about 2.2% of her time in this activity over the year and cub 1 and cub 2, 4.6% and 3.3% respectively. Feeding on the caribou cow and calf noted in the previous section constituted over 98% of tabulated carcass feeding activity for the entire family unit while ground squirrels made up the remainder. Since the sow may well have consumed a greater weight of ground squirrels than of caribou over the year, a discrepancy obviously exists in time spent on feeding on ground squirrel carcasses verses feeding on caribou carcasses. This discrepancy is due to the nature of these 2 activities and the sampling methods. The caribou carcass feeding occurred in open, relatively unobscured terrain over a long period of time and was observed in its entirety. By the nature of its large body structure, it took relatively longer to tear it apart, pull meat off, and gnaw remaining scraps from the bones. In contrast, the ground squirrels obtained by the sow were much more difficult to observe. Episodes were seldom directly observed in their entirety and

ground squirrels were quickly consumed whole. Observations were mostly made in the fall when darkness, distance and weather were much greater problems and holes often were partially obscured by terrain, vegetation, dirt piled up by the sow, or by the sow as she wedged herself in the hole she was digging. Moreover, as noted, the sow appeared to consume ground squirrels in the hole. Clear successes where she was observed actually consuming a ground squirrel were generally brief and often appeared to have been only the tail end of such activity - emerging only as she was wolfing down the last remains. Only in 1 of the 4 clearly observed successes was feeding duration known to be over 30 seconds and since observed durations of activities were rounded to the nearest minute even most of these clear successes were not tabulated as a part of feeding time. Ground squirrels, probably normally were consumed by the sow in under a minute. The cubs, which were much more easily observed when they consumed ground squirrels, took about 3 minutes per ground squirrel.

Carcass feeding, almost entirely as a result of the caribou consumption noted, made up 8.5% of the sow's observed feeding activity in early summer, 18.7% of cub 1's and 14.4% of cub 2's. The percent of time spent by the sow in carcass feeding was much less than that of the cubs as a result of her spending nearly as much time covering the carcass as she did feeding on it. The difference in time spent between the cubs was due to cub 1 eating more and resting less than cub 2. While the caribou was available to them, the bears ate little, or nothing else. The family eventually was chased off the carcasses by a large boar (see Intraspecific Interactions).

Behavior

Perhaps because of the abundant supply of caribou for all, the family generally seemed to share the carcasses quite amicably between them. Only one aggressive attack was noted (by cub 1 on cub 2) and it occurred after most of the carcass had already been devoured.

The sow appeared to have no trouble tearing off and consuming pieces of the caribou. The cubs on the other hand often had to work to tear off the pieces they desired. Cub 1 when feeding would sometimes use one, and at other times both paws when tearing at flesh. Sometimes he would use his weight as leverage, pulling with both paws as when overturning root mats in the spring. Often he would shake his head around vigorously while biting into the flesh to tear off a piece; much like a dog worrying a bone.

When consuming a ground squirrel, the cubs appeared to use their paws to hold it down while they tore off pieces with their mouth. The sow appeared either to consume the ground squirrel in its entirety or in large chunks - wolfing it down with only minimum chewing to crush the bones before she swallowed. The sow appeared to have wolfed down her food when observed feeding outside the hole to prevent theft by the cubs. The sow did not wolf down the abundant flesh from the caribou carcass nor did she ever try to block the cubs from it or defend it. Murie (1981) noted that bears generally bite off small pieces of ground squirrels and consume them with much chewing. This is probably the more usual feeding style of grizzlies when no defense of this small prize is needed. The wolfing style observed here may well be much more typical of sows with cubs.

## NURSING

### Methods

Nursing was defined as active suckling. All noted instances were recorded for the sow and young individually and durations were rounded off to the nearest minute. The time spent nursing by each family member was tabulated seasonally and yearly as were the number of occurrences and the average length of occurrences for nursing bouts observed in their entirety. Nursing was examined as a percentage of each of the cub's total feeding time and for each family member as a percentage of the total time directly observed. Frequency of nursing (in hours/occurrence and occurrences/day) and mean interval between nursing were calculated for each family member, both seasonally and yearly. Frequency in hours/occurrences is actually inverse frequency (1/f) but for simplicity is referred to in the text as frequency.

Activities immediately preceding and succeeding nursing bouts were examined for each bear to help identify patterns of activity associated with nursing behavior. For ease of tabulation and presentation, all activities other than resting were lumped together as 'active' and comparisons were made between active and resting associations. Action-associated nursing bouts were considered to be those in which the particular bear was active prior to nursing and was again active after nursing. Rest-associated nursing bouts were considered to be those in which nursing occurred at the beginning of, during, or at the end of a resting period. Action-associated periods were made up largely of feeding activity. For both action- and rest-associated nursing bouts the average

duration and percent occurrence of each type were examined seasonally and yearly.

A modification was made in the breakdown of seasons for nursing compared with other behaviors as a result of the termination of observed nursing behavior after 18 August. Spring, early summer, and late summer seasonal periods were examined as usual. The normal early fall and late fall periods were redivided into periods prior to the end of nursing (9 to 18 August or the first third of early fall) and after the end of nursing (19 August to 8 October, or the remainder of early and all of late fall). This redivision allowed a better resolution of what was occurring in this last period of nursing in terms of frequency, percent of total activity and of percent of feeding activity (for the cubs) as contrasted with previous seasonal periods. Statistical tests used follow Conover (1971).

## Results and Discussion

### Introduction

Nursing provides the sole source of nourishment for the cubs during their initial period of postnatal development. When cubs are able to forage nursing still provides a valuable supplement to the diet of the growing young. Bear milk contains high concentrations of fat (22.3%), proteins (11.1%) and minerals (1.5%) and has a high caloric content (250 kcal/100g based on Jeness et al., 1972). This milk is the only food the sow actively provides for the young bear, though the cubs may at times feed incidentally on food items the sow has caught or uncovered. Young

bears in the study area remain with the sow until they are 2+, 3+, or more rarely, 4+ years old (Reynolds, 1980).

Yearly Observations

The sow nursed her 2 cubs from the first spring observations in late May until 18 August. Over this period, 32 instances of nursing were observed, 28 in their entirety. Cub 1 was observed nursing 31 times and cub 2, 29 times. The only instance in which cub 1 was not observed to nurse was one in which only a partial observation was made at what appeared to be the end of a nursing period; cub 2 was finishing nursing (she nursed slightly over a 1/2 minute more) and cub 1 was walking away and had probably nursed as well. Cub 2 missed nursing on 3 occasions. On 2 occasions, she was feeding and apparently was unaware of the opportunity. On the third occasion, cub 2 was resting by the sow while cub 1 nursed. It is uncertain whether cub 2 had just nursed prior to cub 1 or simply did not nurse.

Average Duration

Nursing bouts observed in their entirety ranged from 2 to 7 minutes (av. 4.8). Similar values have been found in Denali National Park. Murie (1981) found average nursing duration of yearlings to be 4.3 minutes and Stelmock's (1981) average for all yearlings was 4.2 minutes. These values are slightly lower than observed for the sow in this study. The difference may be accounted for by the inclusion of partially observed nursing occurrences in their data. This was the case at least with Stelmock's data (pers. comm.). The average for the sow in my study was

4.4 minutes if nursing occurrences not observed in their entirety are included.

Stelmock (1981) found no significant difference in mean nursing duration between age classes of young.

The young did not always nurse simultaneously. Average duration of nursing for cub 1 and cub 2 over the year was 4.6 minutes and 4.4 minutes respectively, and were not significantly different (Wilcoxon Signed Rank Test, $T = 5$, $n = 7$, $P \simeq 0.08$). Seasonal average duration of nursing for each family member is tabulated in Table 7.

Associated Activities

Nursing tended to be associated with other activities. These associations were classified into those associated with active periods and those associated with resting periods (Table 8). Overall, nursing for each family member tended to be associated with resting much more than with active periods. Since nursing occurred mostly within or at the beginning or end of resting periods and since a large portion of resting periods were not directly observable because the bears were frequently either partially or totally hidden at these times (see Resting), there was a bias against observing nursing activity associated with resting in the data obtained from direct observation. As a result, the percentages of time spent nursing and frequencies of nursing (noted in the following sections) are probably lower than actually occurred. This was particularly true of late summer when extensive vegetative growth tended to hide the family while resting.

Table 7. Yearly and seasonally observed nursing parameters for the family group: average duration, percent of time observed, percent of feeding time (for cubs), and frequency of bouts.

| | Sow | | | | |
|---|---|---|---|---|---|
| | n* | Average* Duration (min) | Percent of+ Total Time Observed | Frequency+ hrs/occ. | occ./day |
| Spring | 10 | 5.2 | 1.5 | 5.1 | 4.7 |
| Early Summer | 11 | 4.7 | 1.2 | 6.2 | 3.9 |
| Late Summer | 2 | 4.5 | 0.2 | 31.3 | 0.8 |
| First 1/3 Early Fall (8/9 - 8/18) | 5 | 4.0 | 1.1 | 6.2 | 3.9 |
| Last 2/3 Early Fall through Late Fall | 0 | - | 0.0 | - | - |
| Nursing Year | 28 | 4.8 | 1.0 | 7.3 | 3.3 |
| Entire Active Year | 28 | 4.8 | 0.8 | 9.5 | 2.5 |
| Early Fall | 5 | 4.0 | 0.4 | 17.6 | 1.4 |

Table 7. Continued

| | Cub 1 | | | | | |
|---|---|---|---|---|---|---|
| | n* | Average* Duration (min) | Percent of+ Total Time Observed | Percent of+ Feeding Time | Frequency hrs/occ. | occ./day |
| Spring | 10 | 4.9 | 1.4 | 2.4 | 5.1 | 4.7 |
| Early Summer | 11 | 4.7 | 1.2 | 2.4 | 6.8 | 3.5 |
| Late Summer | 2 | 4.0 | 0.2 | 0.3 | 31.3 | 0.8 |
| First 1/3 Early Fall (8/9 - 8/18) | 5 | 4.0 | 1.1 | 1.8 | 6.2 | 3.9 |
| Last 2/3 Early Fall through Late Fall | 0 | - | 0.0 | 0.0 | - | - |
| Nursing Year | 28 | 4.6 | 1.0 | 1.7 | 7.6 | 3.2 |
| Entire Active Year | 28 | 4.6 | 0.8 | 1.2 | 9.8 | 2.5 |
| Early Fall | 5 | 4.0 | 0.4 | 0.6 | 17.6 | 1.4 |

Table 7. Continued

| | Cub 2 | | | | | |
|---|---|---|---|---|---|---|
| | n* | Average* Duration (min) | Percent of+ Total Time Observed | Percent of+ Feeding Time | Frequency hrs/occ. | occ./day |
| Spring | 9 | 4.7 | 1.1 | 1.9 | 6.6 | 3.6 |
| Early Summer | 11 | 4.3 | 1.1 | 2.4 | 6.2 | 3.9 |
| Late Summer | 2 | 4.5 | 0.2 | 0.3 | 31.3 | 0.8 |
| First 1/3 Early Fall (8/9 - 8/18) | 5 | 4.0 | 1.1 | 1.9 | 6.2 | 3.9 |
| Last 2/3 Early Fall through Late Fall | 0 | - | 0.0 | 0.0 | - | - |
| Nursing Year | 27 | 4.4 | 0.9 | 1.5 | 8.1 | 3.0 |
| Entire Active Year | 27 | 4.4 | 0.7 | 1.1 | 10.5 | 2.3 |
| Early Fall | 5 | 4.0 | 0.4 | 0.6 | 17.6 | 1.4 |

*Using the number of nursing bouts which were observed in their entirety.

+Using all nursing bouts, both fully and partially observed.

Table 8. Percentage of nursing bouts associated with rest periods verses those associated with active periods.

| | Sow | | Cub 1 | | Cub 2 | |
|---|---|---|---|---|---|---|
| | % Rest Associated | % Active Associated | % Rest Associated | % Active Associated | % Rest Associated | % Active Associated |
| Spring | 100% (n = 13) | 0 | 92% (n = 12) | 8% (n = 1) | 100% (n = 10) | 0 |
| Spring* | 100% (n = 4) | 0 | 100% (n = 4) | 0 | 100% (n = 2) | 0 |
| Early Summer | 83% (n = 10) | 17% (n = 2) | 82% (n = 11) | 18% (n = 2) | 83% (n = 10) | 17% (n = 2) |
| Late Summer | 50% (n = 1) | 50% (n = 1) | 50% (n = 1) | 50% (n = 1) | 50% (n = 1) | 50% (n = 1) |
| First 1/3 Early Fall (8/9 - 8/18) | 60% (n = 3) | 40% (n = 2) | 60% (n = 3) | 40% (n = 2) | 40% (n = 2) | 60% (n = 3) |
| Last 2/3 Early Fall through Late Fall | - | - | - | - | - | - |
| Nursing Year* | 78% (n = 18) | 22% (n = 5) | 77% (n = 17) | 23% (n = 5) | 71% (n = 15) | 29% (n = 6) |
| Nursing Year | 84% (n = 27) | 16% (n = 5) | 77% (n = 25) | 23% (n = 6) | 79% (n = 23) | 21% (n = 6) |

*Excludes the period 5/20 - 6/1 when the sow was recovering from immobilization and surgery.
n = number of occurrences observed both partially and in their entirety.

Duration of action-associated and rest-associated nursing bouts over the year were compared (Table 9). Using the Mann-Whitney Test action-associated nursing bouts were found to be significantly shorter than the rest-associated nursing bouts for the sow at the 1% level ($T = 10$, $n = 5$, $m = 23$). Reasons for this difference are uncertain but may be due in part to the sow deliberately cutting short nursing bouts because she wished to resume feeding. Nursing associated with active periods, in other words, may have tended to be more 'on the run'.

Percentage of Time Spent

The sow spent about 0.8% of observed time nursing the cubs over the entire active year and about 1.0% over the nursing year from 28 May to 18 August.

Nursing as a percentage of the cubs' total feeding time made up 1.2% of cub 1's and 1.1% of cub 2's feeding time over the entire active year and 1.7% of cub 1's and 1.5% of cub 2's over the nursing year.

Yearly and seasonal nursing percentages for the family members are shown in Table 7. In the spring nursing appeared to be at its highest level. In early summer nursing decreased slightly. In late summer the data suggest a drastic drop in the percentage of time nursing occurred. The extent of this drop, however, may be due in part to the abundance of mosquitoes in the period of observation (13 July through 17 July). Clouds of mosquitoes accumulated that were thick enough to require my use of a head-net to prevent inhalation of them. Quite possibly they may have constituted a similar harassment problem for the bears when they stopped for any length of time. This may have resulted in a severe

Table 9. Average duration of nursing bouts associated with resting periods verses those associated with active periods (in minutes).

| | Sow | | Cub 1 | | Cub 2 | |
|---|---|---|---|---|---|---|
| | Rest Associated | Active Associated | Rest Associated | Active Associated | Rest Associated | Active Associated |
| Spring | 5.2 (n = 10) | - | 4.9 (n = 9) | 5.0 (n = 1) | 4.7 (n = 9) | - |
| Early Summer | 5.2 (n = 9) | 2.5 (n = 2) | 4.8 (n = 9) | 4.5 (n = 2) | 4.3 (n = 9) | 4.0 (n = 2) |
| Late Summer | 5.0 (n = 1) | 4.0 (n = 1) | 4.0 (n = 1) | 4.0 (n = 1) | 5.0 (n = 1) | 4.0 (n = 1) |
| First 1/3 Early Fall (8/9 - 8/18) | 4.3 (n = 3) | 3.5 (n = 2) | 4.3 (n = 3) | 3.5 (n = 2) | 4.0 (n = 2) | 4.0 (n = 3) |
| Last 2/3 Early Fall through Late Fall | - | - | - | - | - | - |
| Nursing Year | 5.1 (n = 23) | 3.2 (n = 5) | 4.7 (n = 22) | 4.2 (n = 6) | 4.5 (n = 21) | 4.0 (n = 6) |

n = number of occurrences observed in their entirety.

(though temporary) curtailment of nursing which normally required a halt of 3 to 6 minutes. Feeding behavior was also noted to be changed during this time, with the sow walking in a fast, highly erratic feeding pattern that was unique in character to this period. This feeding behavior was also suggestive of mosquito harassment. Further supporting the idea of a temporary reduction of nursing due to mosquito harassment is the rise in nursing activity noted for the next period, after mosquito harassment ceased. During the last nursing period, in the first third of early fall (9 August through 18 August), nursing as a percentage of total seasonal activity was nearly the same as in early summer and values were much greater than those obtained in late summer during the peak of mosquito abundance.

A similar spring through fall trend was observed for nursing as a percentage of feeding time for each of the cubs (Table 7). Nursing as a percentage of feeding between early summer and the first third of early fall decreased, largely as a result of the longer periods devoted to other feeding activities in the early fall without a corresponding increase in the frequency of nursing.

Frequency

Expressed as occurrences per day the sow nursed her cubs an average of about 2.5 times per day over the entire active year and about 3.3 times per day during the nursing year (Table 7).

Seasonal frequencies were also examined for each family member (Table 7). The overall frequency pattern appeared to be one of highest incidence of nursing in the spring, a slightly lower incidence in the

early summer, followed in late summer either by values similar to early summer, with a sharp drop at the peak of the mosquito season, or by a more gradual decrease from early summer values peaking around mid-July at the height of the mosquito season and gradually increasing again to early summer values by early fall. Frequencies during the first third of early fall appeared to remain at the same level as early summer right up until cessation of observed nursing activity. Frequencies per day for the sow were roughly 5 in spring, 4 in early summer, 1 in late summer and 4 in the first third of early fall.

Mean Interval

Twelve intervals were recorded in which it was certain that no nursing could have occurred. The mean intervals for the sow, cub 1, and cub 2 were 3.74, 3.73, and 3.65 hours respectively. Intervals for the sow ranged from 2.2 to 5.8 hours. A mean nursing interval also was tabulated which included 3 other nursing intervals in which the family was temporarily hidden for a short period of time and nursing could conceivably have taken place but was unlikely to have done so. This mean interval was 4.60, 4.65 and 4.66 hours respectively for each family member. Intervals for the sow here ranged from 2.2 to 8.3 hours.

If the family group could be watched constantly over the nursing year the mean interval between nursings (in hours) would be roughly equivalent to the frequency (in hours/occurrence) over the nursing year. However, because the bears were observed in varying blocks of time over only a portion of the nursing year (approximately 11%) mean interval is a sample only of those observation periods in which 2 or more nursing

bouts were observed, and excludes all those periods in which only 1 or no nursing bouts were observed. Mean intervals between nursings thus tend to be shorter than frequency. Mean intervals also tend to be shorter for another reason; the longer the actual interval between nursing the more chance there will be breaks in observations (during which the family is hidden for a short time) during which nursing could have occurred and the more likely it is to be excluded from tabulations of the mean interval. Because of these biases, frequency would seem to be a much more valuable tool in sampling.

However, mean interval rather than frequency has been used in other literature discussing nursing and is used here for comparative purposes. Murie (1981) found mean intervals of 2.01, 2.62 and 3.55 hours for sows with spring cubs, yearlings and 2-year olds respectively in Denali National Park. Based on his data the overall average was 2.82 hours. Nursing intervals for yearlings ranged from 1.17 to 5.00 hours and from 0.15 to 9.33 hours for all age groups combined. Stelmock's (1981) mean intervals were 3.4, 2.0 and 2.6 hours for sows with spring cubs, yearlings and 2-year olds in Denali National Park with an overall average of 2.7 hours per family unit. Murie's (1981) data suggest an increase in mean interval between successive age classes of young while Stelmock (1981) found no significant difference between mean intervals of age classes. The lower mean interval (3.74 hours) found in my study of a sow with yearlings is greater than that found for any age group in the Denali studies. Reasons for this are unclear. The longest continuous observation period in which it was known that the sow did not nurse was

9.95 hours and occurred in early summer. The actual interval between nursing may have been longer.

Fall Nursing Termination

Since increasing darkness in the early fall prevented 24 hour watches, it is possible that nursing during this time could have switched over exclusively or almost exclusively to nocturnal periods and may have continued at these times. It seems much more likely however that nursing did in fact either cease entirely or was drastically reduced in frequency at this time. A similar occurrence was also noted for grizzlies in Denali National Park by Stelmock (1981) who observed that nursing frequency decreased greatly for all young in late summer and fall. He suggests that all net energy may be invested in fat deposition at this time and that because berries are readily available, the sow may instead use the energy consumed in lactation for her own fat deposition. R. Hugie (pers. comm., cited by Sizemore, 1980) also noted that Maine black bears may or may not nurse during the fall depending on the quantity or quality of food available and that nursing continued longer in lower quality habitats and during poorer food producing years. Other evidence in the literature seems to suggest that North American grizzly sows with young, who do not breed that summer, typically cease nursing their young for the remainder of the active year sometime between mid-July and late September. The latest date that could be found in the literature of a nursing or lactating grizzly sow in North America was 18 September for a sow with 3 spring cubs by Murie (1952) and 13 September for a sow with 1 yearling by Murie (1981), in Denali Park. This was followed by a

single observation by Stelmock (1981) of a family with 2-year old young nursing on 12 September in Denali Park (no other incidents were observed by him to occur in September), an observation by Harry Reynolds (pers. comm.) of a sow in the foothills of the northeastern Brooks Range, Alaska with 2 cubs of the year which appeared to be lactating on 5 September and a milk sample obtained from a sow with one spring cub on 3 September by Jenness et al. (1972) in Yellowstone National Park. Servheen et al. (1979, as cited by Sizemore, 1980), reported that brown bear females in the Mission Mountains of Montana with young of the year were not lactating by October. Hensel et al. (1969) notes that of 11 females with cubs of the year captured in July all appeared to be lactating. He also notes that of 10 females with yearlings examined in July or August 7 were lactating and had substantial quantities of milk. Two other sows with yearlings examined in July had little milk left and a third appeared to have ceased lactation altogether. This last case, however, may have been a result of the female preparing for breeding which Hensel suggests continues through at least mid-July. In addition to the lactating sow with cubs of the year noted above by Harry Reynolds (pers. comm.) in the foothills of the northeastern Brooks Range on 5 September, 3 other sows with young were examined by him in early fall and late fall. Based on the condition of the mammae (small, flat, little or no milk) all had ceased lactation. One was a sow with 2, 2-year olds from the foothills of the Northwestern Brooks Range (my study area) which was examined on 18 August. The remaining 2 were sows with 2 yearlings from the foothills of the northeastern Brooks Range which were examined on 29 August and 2 October respectively. All this suggests that nursing by non-breeding

females is normally terminated for the active year between mid-July and late September.

Overwinter Nursing

Contrary to what has been thought strong circumstantial evidence, also suggests that nursing does not occur during the inactive period following winter denning, although nursing is again observed in the spring. Folk (1974) attributes the higher heart rates observed for young bears in their winter den to nursing - but does so largely on the basis of observations of a sow nursing the same young in the fall and the following spring. Observations of older young nursing in the spring and summer are fairly common in the literature for sows which do not breed that year. Craighead and Craighead (1973), Murie (1981) and Stelmock (1981) have indicated this to be routine behavior in grizzly families rather than isolated incidents. Hensel, et al. (1969) and Pearson (1975), while not observing nursing, have documented lactation as commonly occuring in sows with older young. The sow in this study nursed her yearlings the following spring as 2-year olds and the spring after that as 3-year olds prior to breeding again (Hechtel, pers. comm.). (Murie [1981] also observed a sow nursing her 2, 2-year old cubs 4 times on 18 May, 2 days prior to family breakup.)

Spring nursing does not necessarily mean that young continue to nurse during hibernation. The evidence mentioned previously suggests that the grizzly sow stops lactating about a month or more before hibernation and it seems doubtful that nursing would resume during winter months. Nursing during winter months seems both impractical and

unnecessary for all but the tiny newborn young which probably can not yet hibernate and would not have the fat reserves necessary if they could. Even the newborn young, born in mid-winter, nurse for only half the overwintering period. It seems improbable that older young would remain awake through the winter as large active young would probably interfere with hibernation by the sow and the energy drain of large nursing young through the winter would be prohibitive in terms of the sow's energy reserves. Nursing of the cubs during hibernation, if it occurs, quite likely would occur only infrequently. To survive without nursing, or nursing only infrequently, the young probably would have to hibernate for most if not the entire winter as does the sow. This idea is supported in part by an observation by Craighead and Craighead (1972) and Krott (1964). Craighead and Craighead examined a den on 28 December, constructed by a sow with 2 cubs of the year. He found all 3 grizzlies lethargic and sleeping. Also while the sow apparently detected their presence and growled, neither cub appeared to rouse until they took flash pictures. The bears apparently still remained lethargic, did not emerge afterward while they were under observation and continued to utilize the den through the winter. The cubs apparently had entered into a normal adult-like deep hibernation pattern and if anything appeared less active than the sow. Krott (1964) raised 2 grizzly bear cubs and found they hibernated throughout the winter months, apparently only awakening when disturbed by him. Hibernation slows heart rate, temperature and overall metabolism and has the advantage of allowing a considerable energy savings (Folk, 1974). Further supporting the idea that young (other than newborn) hibernate and do not need to nurse is an

observation by Craighead and Craighead (1972) of an orphaned spring cub in Yellowstone National Park which successfully denned and overwintered by itself. Krott's spring cubs also successfully overwintered without nursing.

The above suggests that hibernation probably is as important to the survival of the young as it is to adult bears. Assuming the young do hibernate, perhaps the most significant evidence against nursing occurring regularly during the winter months comes from metabolic studies of the physiology of hibernation. Nelson (et al. 1973; 1980; et al. in press) found hibernation in bears to be characterized in part by an extraordinary metabolic system in which no lean body mass is lost, there is no buildup of toxic wastes and in which fat reserves alone are used to provide needed energy and produce essential water. This unique biochemical process was found to occur throughout the winter hibernation period and continued fully or at least in part for 10 days to 3 weeks following spring arousal. It was found, however, that protein intake during hibernation would clearly disrupt these well balanced but delicate biochemical reactions of hibernation. Since bear milk is characteristically high in protein it is likely that regular, persistent nursing would interfere with the young's ability to hibernate and thus to conserve energy and retain lean body weight, and might well hinder their ability to survive over winter. Adult bears typically do not eat, drink, urinate or defecate during hibernation, even when aroused and food and water are available (Folk, 1974).

The grizzly cubs raised by Krott (1964) once they had fully entered hibernation typically refused food and did not urinate or defecate.

Only on one occasion well into the winter was food (meat scraps) accepted and consumed and snow eaten. The effect if any of this limited consumption on hibernation is unknown. When rechecked 2 to 3 weeks later, however, both appeared to again be hibernating and continued to do so for another month.

Kingsley (in press) presents the only other evidence I have found for overwinter nursing. He notes that older females (15+ years) lose about 43% of their fall weight over winter while males lose only 20%. He speculates this is due to the extra energy used for gestation and lactation overwinter. He does not however indicate reproductive status of sows or age of young if any, and does not give examination dates other than they occurred in May and June for spring and August or September for fall.

Pearson (1975) weighed 2 adult male and 2 subadult female grizzly bears shortly before denning and upon emerging. He found the percentage of weight loss of both adult males to be about 30%, versus Kingsley's 20%, and those of the 2 subadult females to be 28% and 43%, respectively. Pearson's information was obtained shortly before denning and right after denning. It eliminates biases inherent in measurements taken well before or well after the overwinter periods. It is possible the adult males examined by Kingsley may have put on weight during April, May or June prior to being weighed. Grizzly males tend to emerge earlier than sows with young and wander far in search of winter-killed animals, sick or injured prey, and any other readily available food source (Bromlei, 1965; Craighead and Craighead, 1974; Quimby, 1974). It is questionable whether differences in overwinter weight loss between males and females are as substantial as reported by Kingsley.

While sows giving birth to spring cubs may have higher average winter energy demands than other bears, it seems likely that adult females with older young have about the same overwinter energy demands as unbred adult females without young, and boars. What extra fat loss does occur in sows with older young, as compared with boars, seems more likely to result from their renewed lactation in the spring, and their much more restricted movements in search of food in the spring (Bromlei, 1965; Crook, 1971) rather than to overwinter loss. Spring is usually a period of food scarcity (Sizemore, 1977; Craighead and Sumner, 1980; Mealey, 1980), especially for the family group. Because the sow and cubs are active and their metabolic rate has returned to its higher normal level, much more energy is required than during hibernation and both the sow and her nursing cubs probably rely heavily on, and substantially drain, the sow's fat reserves through this time (see following section).

Energy Cost of Lactation

Hanwell (1977) determined that in general energy output in milk is a function of body weight, and has calculated (based on data from 19 species of lactating mammals) energy output in milk (kcal/day) to be 127.2 x body weight (kg) $^{0.694 \pm 0.041}$. Using an estimated body weight for the sow upon emergence in the spring of 110 kg energy output is 3321 kcal/day, with a range from 2739 to 4026 kcal/day at the 95% confidence level. Assuming that the sow in the spring is relying almost entirely on her fat reserves to produce milk the sow would use from 0.30 to 0.45 kg of her fat per day in milk production alone (using 1 kg fat = 9000

kcal). Bears are normally in a negative energy balance in the spring; hence the energy loss for female grizzlies with young must be substantial. Assuming that the sow in the study nursed her cubs from time of emergence in spring (about 7 May) until the end of spring she would have lost 10 to 15 kg of body fat due to milk production alone over this period.

A similar though perhaps smaller energy drain due to lactation probably occurred over the remainder of the nursing year. However, with the beginning of the vegetation growing season, movement of caribou into the area, and increasing availability of ground squirrels in early summer, the sow was able to move into a positive energy balance despite this drain (she gained 14 kg from 29 May to 24 June and 13 kg from 24 June to 8 August [Reynolds, 1980]). It seems likely based on the figures above, and the seasonal variations in nursing, that the sow used 25 to 45 kg of fat energy over the nursing year in milk production for her young.

Strategy of Seasonal Patterns

Though nursing in this study made up little more than 1% of the yearling's total feeding time during the entire active year its strategic biological importance is great. The sow's milk contains high concentrations of fat, protein and minerals, and has a high caloric content. In the spring when the young were in a negative energy balance because of low food availability, and their fat reserves had been greatly depleted over the winter, it provided a nourishing supplement that helped see them through this period. The sow, though in a negative energy balance herself, appeared to be able to get along with less difficulty than her

young in the spring. This is partly because the metabolism of adult bears (based on heart rate) is both slower and more efficient than that of young bears during hibernation (Folk, 1974), so a sow probably uses relatively less of her fat reserves over the winter than her young. The sow was also a much more effective forager than her yearlings throughout the year, especially prior to the growing season when roots had to be dug out of the ground. Because a sow normally has proportionately greater fat reserves than her cubs and can obtain foods much more easily at this time, it is biologically advantageous to allocate more of her resources to the young in the form of milk to help ensure their survival at this critical period (provided she has sufficient resources so that her own survival is not threatened).

Nursing also provides a continuing high protein, energy rich supplement during the summer when the cubs are growing and putting on lean body weight. Protein and calcium are especially needed by the young for growth at this time and external sources in the form of easily assimilated animal protein are available only sporadically. Such sources are much more accessible to the sow who can in turn maintain a more continuous supply to the cubs in the form of milk. During August berries ripened in the study area and the bears, especially the cubs, appeared to spend more time feeding and fattening on berries in preparation for the winter. Fat laden ground squirrels also became much more readily accessible, especially to the adult, and were much more actively sought. With winter approaching, fat deposition would seem to become more important to survival than lean body growth and nursing would lose much of its benefit to the young if, as is usually the case, abundant quantities of

berries are readily available. It would seem more advantageous if the protein, minerals and energy previously devoted by the sow to lactation were utilized instead to replace any protein and mineral debits, and to enhance fat deposition to support her through the winter and to help support the entire family through the following spring. The sow and young under study appeared either to stop nursing abruptly or at least to reduce nursing drastically beginning about 19 through 21 August. The literature suggests that all non-breeding grizzly sows with young (of any age class) normally cease nursing or lactating between mid-July and late September (see previous discussion: Fall Nursing Termination). Several possible triggering mechanisms could halt lactation, from lack of interest by the young, to seasonal environmental cues. Timing of cessation of nuring may correspond to availability of alternate food sources for the young such as berries. If the scenario I suggested previously is correct, nursing does not resume during the inactive winter months. Instead both the sow and young conserve their fat reserves by hibernating throughout the winter and the extra reserves of the sow are used for family support in the spring.

Nursing Attempts

A nursing attempt was defined as behavior in which a cub tried to suckle. Some difficulty was encountered in identifying such attempts, since observations were generally made at distances that did not readily allow determination of vocalizations or body language that may have been used in such attempts. (Vocalization may occur at times in both grizzly and black bear cubs when suckling attempts are not immediately granted

[Murie, 1981; Pruitt, 1974] and body language has become recognized as an important component of social communication in both grizzly bears and black bears). Only overt behaviors could be quantified and therefore only a partial picture of nursing attempts could be provided. Overt behaviors used by the young in attempts to suckle included: (1) remaining near and watching the sow; (2) remaining near and watching the sow culminating in what could be called brief, low keyed harassment; and (3) actively harassing the sow. Two nursing attempts whose type was not recorded were classified as unknown. The cubs generally appeared to assume submissive attitudes during these attempts at nursing though occasionally they were quite aggressive. These submissive attitudes, which involved both facial expressions and body postures, were not readily quantifiable at a distance.

In remaining near watching, the young would either feed or travel toward the sow and follow her around closely as she fed and/or sit or stand by and watch her - or, if the sow was resting, walk around her, sometimes sniff her and/or sit or lay by her watching her. They seemed to be unobtrusively letting the sow know they were there, waiting for the sow to make herself available to them. The cub(s) generally seemed hesitant about intruding on the sow in these attempts. Although the young frequently would feed near the sow and briefly look at her submissively and appear to wish to nurse, only those occasions where intensity and duration made it obvious was it tabulated as a nursing attempt. As a result of attempting to include only behaviors that were clearly a nursing attempt in this category a number of actual attempts probably were left out and it is likely that this category is underrepresented.

Many of these questionable attempts may not have constituted serious attempts at nursing, since they were not obvious to me and they may have not been obvious to the sow who was generally either busily engaged in feeding or was resting.

The next type of nursing was basically the same as remaining near watching, except that the cubs eventually appeared to lose patience and became slightly bolder when the sow did not make herself available and instead of giving up, tried more actively to make their presence and desires known. This was accomplished by briefly pawing, nuzzling, or licking or by a direct nursing attempt. This was usually done in a slow, gentle, hesitant manner but occasionally it was more aggressive. This type was noted predominantly when the sow was resting and perhaps the cubs felt she may have missed their more subtle overtures. Licking was noted only once; it was directed to the sow's face.

The third type, active harassment, was the most intense and involved 1 or more harassment techniques that directly intruded on the sow's activity. Such techniques included direct nursing attempts on the sow's mammae, moving in front of the sow if she was active, repeatedly pawing or nuzzling her, or occasionally, even nipping her. Frequently the other forms of active harassment culminated in direct nursing attempts. The simple direct nursing attempt, continuously repeated, was probably the most aggressive harassment tactic commonly utilized. While the harassment category involved behavior patterns considerably more aggressive than the other categories these behaviors still appeared to have submissive aspects to them. Frequently the cubs seemed to try the sow's patience but no clear case of retaliation was seen.

Eighteen overt nursing attempts were observed over the year. Of these 61% were made by cub 1 alone, 33% by cub 1 and cub 2 in combination and 6% by cub 2 alone. Attempts by cub 1 alone were successful only 9% of the time while those involving both young were successful 67% of the time. The single instance involving cub 2 alone was unsuccessful. The joining of forces by both yearlings in a nursing attempt appeared to be the single most influential factor in obtaining a favorable response.

Over the year, 78% of all directly observed nursing occurrences were associated with the sow's resting periods (excluding the recovery period 30 May to 1 June. Of those attempts made at times other than when the sow was recovering from surgery, 64% were made while the sow was resting and only 36% while she was active, despite the fact that the sow was active about 59% of the time over the nursing year and despite the family being largely hidden during many rest periods and attempts unobserved. Success rate for all attempts made when the sow was active was 20% and when the sow was resting was 33%. The greater proportion of attempts by the young when the sow was resting may reflect a learned association of nursing with the sow resting and perhaps the somewhat greater success of their attempts at these times.

No conclusions could be drawn concerning the value of one category of nursing attempt versus another because of the small sample size of successful nursing attempts.

The sow's reactions to nursing attempts were varied. One such reaction was to allow the young to nurse immediately. Much more commonly she responded with a variety of basic behavioral patterns that discouraged

attempts to nurse - even if she eventually allowed them to nurse. Six such basic avoidance patterns were observed, the first 4 being the most common. These are:

1. Move Off. This occurred when the sow was either resting or active and was disturbed by an attempt. If resting, she got up and moved away, sometimes resuming resting very shortly afterward and other times becoming active. If disturbed when active, she moved away from the cub(s), though usually not very far. With repeated disturbance she would repeatedly move off.
2. Turning Away. This occurred both when the sow was resting and when she was active. If she was resting she would simply turn away from the cub(s) or shift so that her mammae were not exposed. When she was active and attempts were made she would turn her back to the young to minimize harassment and/or prevent direct nursing attempts.
3. Move Off, Turning Away. Or vice versa. This pattern was simply a combination of the last 2 patterns.
4. Ignore. In this type the sow simply paid no attention to attempts by the young though she was clearly aware of them. Sometimes this was her total reaction (or nonreaction) and other times it followed other avoidance behavior such as turning over when she was resting. Sometimes it occurred between other avoidance behaviors. Typically, ignoring occurred only when attempts were low keyed or harassment mild. Unwelcome direct nursing attempts were responded to with other types of avoidance behavior.
5. Push Away with Paw. This was observed only once. The sow was resting with the yearlings beside her and cub 1 had just stopped

nursing a minute prior. Cub 1 attempted to resume nursing and the sow gently pushed him away with her paw.

6. Aggressive Response. Actually no clearcut aggressive behaviors were observed in response to the yearlings' attempting to nurse no matter how aggressive these attempts. The sow was not observed to strike, bite or even overtly threaten her young except for one questionable incident. This incident is discussed in the section on Aggression.

Mean interval between nursing and the next nursing attempt was computed to obtain an idea of the cub's preferred nursing interval compared to that actually allowed by the sow. Only those intervals without breaks in observation in which nursing could possibly have occurred are included. The mean interval was 2.12 hours for cub 1 alone (5 intervals), 2.17 hours for cub 1 and cub 2 together (1 interval), and no intervals were observed for cub 2 alone. The overall average interval between nursing and nursing attempts was 2.13 hours (6 intervals) with a range from 0.02 to 3.92 hours. This overall mean interval is more than 1 1/2 hours less than the yearly mean interval between nursing which is approximately 3.7 hours and suggests that the cubs (or at least cub 1) would have preferred to nurse on a much more frequent basis than they were allowed to. This is further supported by evidence in later sections.

## Nursing Initiation

Instances of initiation of nursing by the young are identical with the successful nursing attempts discussed in the last section and will not be discussed again in detail here. Initiation of nursing bouts by

the sow appeared to take the form of simple postural shifts - either rolling on her back or turning on her side. Problems arose in clearly identifying nursing initiations by the sow, however. When the cubs came near, or were near her, and the sow assumed a nursing posture it was in many cases difficult or impossible to tell whether it was the sow who had initiated the nursing bout or whether the cubs had initiated the bout through cues I could not see or hear. Only overt behaviors could be quantified.

Eleven obvious nursing initiations were noted and 6(55%) appeared to be initiated by the sow. Cub 1 and cub 2 jointly initated 4(36%) observed nursings and cub 1 initiated 1(9%) nursing. No instances were observed where cub 2 initiated nursing.

The duration of nursing may be related to which bear or bears initiated the nursing activity (Table 10). Average nursing duration for each of the family members tended to be shortest when initiated by the sow and longest when initiated by both cubs jointly. This may be due to a lesser intensity of interest on the part of the cubs when it was the sow's offer rather than their own desire causing them to ask. Sample size is too small for firm conclusions. Differences were not significant when examined using the Mann-Whitney Test ($T=6$, $n=6$, $m=4$, $P \simeq 0.11$).

Nursing Position

The sow usually assumed 1 of 2 positions when nursing her 2 yearlings, either lying on her back (87% of observations) or lying on her side (13%). On one occasion the sow called the cubs to her and assumed a sitting-leaning-back position from which they started to nurse, but

Table 10. Average duration of nursing bouts* as a function of the bout initiator.

| | Sow | | Cub 1 | | Cub 2 | |
|---|---|---|---|---|---|---|
| Initiator | Occurrences (n) | Average Duration (min) | Occurrences (n) | Average Duration (min) | Occurrences (n) | Average Duration (min) |
| Unknown | 17 | 4.8 | 17 | 4.5 | 17 | 4.3 |
| Sow | 6 | 4.3 | 6 | 4.3 | 6 | 4.3 |
| Cub 1 | 1 | 5.0 | 1 | 5.0 | - | - |
| Cub 2 | - | - | - | - | - | - |
| Cub 1 and Cub 2 | 4 | 5.3 | 4 | 5.3 | 4 | 4.8 |
| Total | 28 | 4.3 | 28 | 4.6 | 27 | 4.4 |

*For nursing bouts observed in their entirety.

she promptly rolled on her back to continue nursing. The sitting-leaning-back position sometimes appeared to be used as an invitation to nursing and/or as a 'ready' position in which the sow remained until the cubs approached closely. The sitting-leaning-back position was typically utilized as a brief transitional position immediately prior to lying on her back. Occasionally when the sow was resting, she would simply roll over on her back to nurse.

Murie (1981) observed nursing positions of grizzly sows in Denali National Park, which correspond to the on-back and on-side positions observed here. He also observed a third type in which the sow nursed her young partially or entirely from a sitting position. He notes that the on-back position is the usual position, which corresponds to observations in this study. Hensel et al. (1969), observed 2 nursing bouts of grizzlies with 2 cubs of the year on Kodiak Island, Alaska one of which was on-side and one of which was from a sitting position. Nursing position is probably a function of the individual preference of the particular sow and as noted by Hensel, of the sow's family size.

Grizzly sows have 2 rows (left and right) of 3 mammae. Pairs of mammae occur in the upper pectoral, lower pectoral, and pelvic areas. When the sow used the on-back position, cub 1 was always observed to nurse on the sow's right side and cub 2 on the sow's left side. When one attempted to suckle on the other side or sometimes merely got too close to the other nursing cub, aggressive encounters between the cubs often took place. Threat vocalizations were heard (during observations in proximity to the family) when one cub or the other appeared to feel its territory threatened. Simply being on the wrong side at the time

the sow offered to nurse could lead to aggressive attacks. It is possible that this same behavior, or a slight modification of it, could partially explain the occurrence in some 3 cub litters of a much smaller runt who is either largely shut out of much nursing or relegated to less accessible or less productive mammae. It is unknown whether the degree of territoriality observed here is common or unusual in grizzly families, since no one has systematically studied any intact bear family prior to this.

Of the 2 recorded incidents where the sow lay on her side and nursed, such right-side, left-side territoriality was not possible. In 1 of these incidents, cub 1 was nursing alone. In the other cub 1 was apparently nursing on the lower pectoral mammae and cub 2 on the upper pectoral mammae. It is unknown whether any territoriality was involved in these on-side positions. When the sow nursed on her side, cub 1's position at the lower pectoral mammae was probably more advantageous than cub 2's at the upper pectoral. In this position cub 1 appeared to have easier access than cub 2 to the sow's mammae because the sow's forelegs appeared to hinder access to the upper pectoral mammae more than to the lower pectoral mammae. In this instance cub 2's nursing was cut short when the sow moved her foreleg and totally blocked cub 2's access. It is possible that the sow usually chose the on-back position to allow the young easy access to all teats and perhaps also to reduce friction between the cubs by allowing each cub an entire side of their own. In the usual on back position, upper pectoral mammae appeared to be used most commonly, followed by lower pectoral mammae, and more distantly by pelvic mammae. Hensel et al. (1969) noted a similar use pattern based on examination of the mammary glands of immobilized

females grizzlies. It is possible this relative usage of the mammae reflects the relative abundance and availability of milk within the set of teats. Hensel et al. (1969) noted that in sows with reduced milk volume, the most noticeable reductions were found in the lower pectoral and pelvic mammae.

In general, when nursing, the young suckled steadily on 1 teat - generally the upper pectoral - with little movement other than slight postural adjustments. Cub 1, however, on many occasions would switch from one teat to another anxiously, as though dissatisfied. Cub 2 did this only seldom. At these times cub 1 would occasionally try to raid cub 2's side and an aggressive encounter ensued. A possible explanation for this may be that, since each cub pretty much had its own supply of milk (the right and left sides of the sow), cub 1 tended to deplete his supply of milk more frequently than cub 2. This seems likely since cub 1 was generally a more aggressive feeder than cub 2 (seen in the much greater number of nursing attempts by cub 1, in the slightly larger number of nursing occurrences by cub 1 and by the slightly longer overall average length of nursing bouts of cub 1). Periodic early depletions of the limited supply of milk may have contributed to the unusually high level of aggression and short tempers associated with this prized food source.

Nursing Termination

Nursing activity may be ended either by the sow or by the cubs. The sow ended the nursing bout either by turning over into a resting position, generally so that mammae were not readily accessible, or by

getting up and moving off. These behaviors were basically the same as avoidance patterns noted previously in nursing attempts by the young. If the sow did not terminate nursing, one or both cubs eventually stopped.

Of those nursing bouts where the terminator(s) of the event was known, 6(30%) involved termination of both cubs by the sow, 5(25%) involved termination of one cub by the sow after the other had finished and in 9(45%) of the bouts both cubs were allowed to nurse until finished. The average duration of nursing (by the sow) for each type was 4.2, 5.0, and 5.1 minutes, respectively. Cub-terminated nursing activity periods, as might be expected, seemed longer on the average than were sow-terminated, but differences were not significant when examined using the Mann-Whitney Test ($T=15$, $n=6$, $m=9$, $P \simeq .08$).

When allowed to nurse as long as it wished, cub 1 nursed on average 4.7 minutes ($n=15$) and cub 2, 4.8 minutes ($n=11$). The average time spent nursing by each cub when allowed to nurse as long as it wished, provides an exact determination of either the average time required to reach satiation of their nursing drives and/or of the average time required to temporarily deplete the sow's milk reserves; probably the latter. Human babies are known to deplete the milk supply of a breast in about 4 to 7 minutes (Vorherr, 1974) and cub 1, as noted, on a number of occasions acted as though he had depleted his milk supply early and anxiously shifted from teat to teat on his side of the sow and appeared frustrated. Differences between cub 1's and cub 2's average nursing duration, when each was allowed to nurse as long as it wished, were not statistically significant when examined using the Mann-Whitney Test ($T=77$, $n=15$, $m=11$).

## TRAVEL, PROXIMITY AND MOVEMENTS

### Methods

Travel (walking or running movements not directly associated with other activity classes such as feeding, play, disturbance or aggression) by the sow involved walking movements, and, by the cubs, involved mostly walking movements. It was distinguished from somewhat similar light feeding and foraging activity by a generally direct line of travel with head up, rather than by walking punctuated with frequent halts, frequent changes in direction and head oriented downward typically associated with feeding and foraging behaviors - and by the lack of specific associated food search patterns such as occurred when locating ground squirrels or chasing caribou. Little or no feeding occurred while traveling; at most, infrequent bites were grabbed along the way with only the briefest of stops or no stops at all. Borderline instances between travel and feeding were categorized as miscellaneous activity and are discussed further in that section. Travel, as with other major activities, was rounded off to the nearest minute and instances of under one half minute were not included in the tabulations.

Average proximity between family members was derived from estimates of observed distances between them, recorded on the hour, or as close to the hour as possible, throughout the observed year.

Average hourly movements were obtained for each family member by estimating the overall point to point movement for each bear, on the hour, from one hour to the next. Such a measurement provided an estimate of straight line movement from one hourly observation of position to the next. This method of measurement obviously does not provide actual

movements within the hour. A bear could conceivably wander about circuitously for a mile or more during the intervening hour but end up in the same place as noted previously. Despite its inadequacies, this method does supply minimum hourly estimates of distances traversed and allows seasonal comparisons of minimum hourly average net movements. This method of estimating movement was particularly valuable in that it required little time and allowed maximum attention to be devoted to the observation and recording of activity patterns and behavior, while still providing valuable information on movements.

Data excludes the period of recovery of the sow from handling unless otherwise noted.

## Results and Discussion

### Travel

Roughly 130 travel episodes were observed for each family member (excluding the recovery period). Travel by the sow predominantly involved movements between feeding areas while travel by the cubs almost entirely involved movements that kept them in proximity to the sow. Yearly and seasonal proportions of travel as a percentage of total directly observed active time for each family member are shown in Table 2 and appear to differ little between family members. Travel made up from as little as about 2% of active time in late summer to as much as about 10% in late fall. Over the year travel averaged about 4% of total active time.

While I originally felt the proportion of time spent in travel by the sow would be significant in that it would probably directly reflect seasonal differences in overall movements, this was not the case.

Travel was a minor component of overall seasonal movements; moreover, travel was not always indicative of the level of such movements either. Movement associated with feeding activity was by far the dominant force in overall movements throughout the year. In late summer, for instance, movements increased considerably from spring and early summer levels, but travel time was at its lowest seasonal level. Movement resulting from feeding activity increased in this instance apparently due to the influence of mosquito harassment which caused the sow to graze lightly at a nearly constant fast walk while time spent in actual travel was probably reduced by the nature of the sow's 'on the run' movements. The increased speed at which the sow moved reduced travel time between feeding areas, as did the apparently smaller intervening distances between feeding areas which resulted from the more continuous lush patterns of vegetation that existed at this time when the sow was mainly feeding on the tops of grasses and sedges.

Types of Travel

Travel by the sow fell into a number of different classifications based on the apparent purpose of each occurrence. These categories include travel between feeding sites, travel between feeding and resting sites, shifts from one resting site to another, getting up during a rest period and moving off to urinate or defecate and moving back again, and travel to the cubs. On a yearly basis travel between feeding sites made up 82.6% of the sow's known travel time, travel between feeding and resting sites 12.6%, resting site shifts 1.9%, moving off to relieve herself 0.7%, traveling to one or both cubs 0.5%, and miscellaneous

travel 1.9%. Unknown travel activity made up 11.3% of total travel time.

On a seasonal basis travel between feeding sites was clearly predominant in every season, making up a low of 64% in late summer and a high of 97% in the fall. Travel to or from resting sites, the next most important category, was only observed from spring through late summer seasons when special sites, such as terraced talus mountain ledges or snow banks frequently were being sought. Later, when sites appeared to be selected predominantly for their handiness, travel time for resting vanished. Travel to or from resting sites during the first three seasons ranged from 14 to 23% of each season's total travel time. No other clear seasonal patterns were observed.

On a yearly basis average travel time per occurrence varied substantially among various types of travel and appeared to show a fairly logical progression between types. Moving off to relieve herself and moving back to rest was the shortest and averaged 1.5 minutes, followed by shifting resting sites and travel to the cub(s) at 2.0 minutes, followed by travel between feeding sites at 3.7 minutes, and travel to or from resting sites at 4.7 minutes.

Travel following immobilization and surgery in the spring was not included in any of the previous tabulations because of the effects of immobilization and surgery. About half the sow's travel time during the three-day recovery period was spent in long periods of slow torturous travel to the cubs to maintain contact with them, while during the remainder of the year travel of this type was practically negligible. Normally during the year the sow did not maintain contact with the cubs

by traveling to them, would seldom halt her travel and wait for them (and then only if the cubs appeared not to have noticed she was traveling) and she seldom appeared to deliberately maintain proximity with the cubs by orienting her feeding direction toward them. The job of maintaining the proximity of the family unit was the cubs' and only under unusual circumstances that may have threatened the cohesiveness of the family unit, did the sow play a direct and major role in maintaining family unity.

Over 98% of the cubs' travel had to do with maintaining proximity of family members and almost all of this with maintaining proximity to the sow. Travel by the cubs was divided into travel between feeding sites, travel between feeding and resting sites, moving off to relieve themselves and moving back to rest, travel to or following the other cub, travel to and/or following (or traveling with) the sow, traveling to and/or following the sow and other cub, and miscellaneous or unknown traveling. 'Traveling to' the sow and/or other cub occurred when one of the cubs had allowed another family member(s) to get fairly far off and refers to traveling to proximity with or greatly reducing the distance to the other family member(s), usually the former. 'Following' or 'traveling with' generally occurred when one family member was noted to have just started to travel and another started traveling with or after the first. Over the year cub 1 spent 1.3% of total travel time traveling between feeding sites, 0.6% traveling to cub 2, 90.0% traveling to and/or following the sow, 7.7% traveling to and/or following the sow and cub 2, and 0.4% in miscellaneous and unknown travel activity. Cub 2 over the year spent 0.8% traveling between feeding sites, 0.2% traveling

to or from a resting site, 0.4% getting up and moving off to relieve herself and moving back, 1.0% traveling to or following cub 1, 96.1% traveling to and/or following the sow, 1.0% traveling to the sow and cub 1, and 0.4% in miscellaneous and unknown travel activity. Differences between the cubs were generally slight. Perhaps the most noticable difference was a slight tendency for cub 2 to start to travel to maintain proximity to the sow before cub 1. Travel by the cubs between feeding sites occurred almost exclusively in the fall.

'Travel to' a family member (almost invariably the sow) tended to be much shorter for the cubs than following the sow, largely because following usually proceded at a leisurely walk, while 'travel to' (since it typically involved closing large gaps in distance to regain lost proximity), often involved running or alternate running and walking.

Travel and Proximity of Family Members

Travel to the sow did not occur when any particular distance accrued between her and the cubs. The cubs could travel to the sow from as little as about 6 m (20 ft), about the minimum distance at which an incident could last 30 seconds or more and be counted as travel (if, for example the sow had just laid down to rest and a cub traveled slowly to join her), or could travel from as far as 370 to 430 m (1,200 to 1,400 ft), as when on several occasions they fed far from the sow when she was first immobilized or in the fall when the sow was frequently covering relatively very large distances in relatively short periods of time. The greatest distance observed between the sow and cubs was reached at these times with the cubs feeding as far as 490 m (1,600 ft) away in the

spring when the sow was incapacitated and with a distance of about 1650 m (5,400 ft) occurring between sow and cubs on one occasion at the end of early fall. Most commonly travel to the sow would occur when distances to the sow reached 60 to 150 m (200 to 500 ft) in the spring or early summer season and 150 to 300 m (500 to 1,000 ft) in late summer through late fall seasons. To make sure that relative proximity was being maintained the cubs periodically monitored the sow's position.

Travel by the cubs, while important in maintaining family proximity, usually was only a portion of behavior maintaining family togetherness. More characteristically the cubs, when active, would feed toward the sow and/or other cub until relative proximity was achieved. Travel by the cubs usually occurred only when distances from the sow were noticed to have become great or when the sow started traveling, so the cubs had to travel to catch up.

The cubs seldom traveled to maintain proximity to each other, relying almost entirely on orienting their feeding movements toward one another before distances between them started to become very great. Their success in so doing is strongly illustrated by the fact that despite travel oriented toward the other cub being neglible compared to travel oriented around the sow, the cubs average yearly proximity to each other was nearly twice as close as was their proximity to the sow.

The play behavior of the cubs also helped in maintaining family proximity. On occasion, the cubs would substitute running play in place of travel to catch up with the sow, and on many occasions from mid-June on, play appeared to be a magnet that temporarily drew the cubs together.

Yearly and seasonal proximities between the sow and cub 1, the sow and cub 2, and cub 1 and cub 2 are tabulated in Table 11. The 3 day recovery period in the spring is similarly tabulated for comparison. Proximities for each pair of family members while resting averaged 3 m (10 ft) or less for all seasons while proximities while active ranged in average distance from as little as 7 m (25 ft) in early summer to as much as 56 m (180 ft) in late fall. Average distances between the cubs while they were active were consistantly less during all seasons than were distances between the sow and cubs and, as noted, average yearly distances between the sow and cubs was nearly twice as great as between the 2 cubs. Greatest average distances between sow and cubs generally occurred when the sow was active and the cubs resting and vice versa.

Shifts in proximities from season to season showed similar patterns for all pairings of family members and appeared to reflect changes in movements, feeding activity, and other environmental influences. In the spring, for instance, feeding on roots distributed in patches and requiring time to overturn, expose, extract, and consume, contributed to somewhat higher distances between family members than in early summer when more continuous new growth allowed feeding distances between family members to be generally smaller.

The sow's selection of remote talus slopes for resting suggests she may have been protecting herself and her cubs from encounters with males. The sow moved much less during the spring and first half of early summer than during the rest of the year, and it is quite possible that the sow's movements were severely restricted at this time for the same reason. Proximities may in turn have been smaller as a result of

Table 11. Average proximity (meters) between family members.

| | Both Active | | | Both Resting | | | One Active, One Resting | | | Activity of One or Both not Recorded | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sow Cub 1 | Sow Cub 2 | Cub 1 Cub 2 | Sow Cub 1 | Sow Cub 2 | Cub 1 Cub 2 | Sow Cub 1 | Sow Cub 2 | Cub 1 Cub 2 | Sow Cub 1 | Sow Cub 2 | Cub 1 Cub 2 | Sow Cub 1 | Sow Cub 2 | Cub 1 Cub 2 |
| Recovery Period | 80[1] | 78[1] | 19[2] | 17[2] | 52[2] | 1[2] | 138[2] | 80[2] | 78[1] | - | - | - | 63 | 63 | 14 |
| Spring* | 18[2] | 18[2] | 12[2] | 1[1] | 0[1] | 2[1] | 30[1] | 10[1] | 15[1] | 30[1] | 53[1] | 34[1] | 15[2] | 16[2] | 11[2] |
| Early Summer | 8 | 9 | 7 | 1[2] | 1 | 2[2] | 5[1] | 3[1] | 6[1] | 8[1] | 8[1] | 6[1] | 5 | 5 | 5 |
| Late Summer | 53 | 46 | 31 | 0[1] | 1[2] | 0[2] | 76[1] | 30[1] | - | - | - | - | 45 | 34 | 25 |
| Early Fall | 28 | 28 | 14 | 3[2] | 2[2] | 2[2] | 59[1] | 102[1] | 17[1] | - | - | - | 25 | 25 | 11 |
| Late Fall | 56[1] | 48[1] | 19[1] | - | - | 0[1] | 76[1] | 76[1] | - | - | - | - | 58[1] | 52[1] | 17[1] |
| Entire Active Year* | 31 | 29 | 17 | 2 | 1 | 2 | 40 | 33 | 15 | 23[1] | 38[1] | 25[1] | 24 | 21 | 13 |
| First 1/3 Early Fall[+] | 14[2] | 14[2] | 12[2] | 3[2] | 2[2] | 1[2] | 3[1] | - | 3[1] | - | - | - | 10 | 9 | 8 |
| Last 2/3 Early Fall[‡] | 35 | 36 | 15 | 4[1] | 2[1] | 2[1] | 70[1] | 102[1] | 24[1] | - | - | - | 35 | 35 | 13 |

*Excluding the recovery period (5/30 - 6/1).
[1]Sample size < 10.
[2]Sample size ≤ 29.
[+]Prior to cessation of nursing (8/9 - 8/18).
[‡]Following cessation of nursing (8/21 - 9/8).

reduced movements making it much easier for the cubs to maintain distances with little effort. Possibly the poor condition of the cubs, especially cub 2, at this time may have limited the cub's ability to follow the sow and may have also been a contributing factor in restricting the sow's movements. It is also possible that closer distances to the sow may have been maintained by the cubs to some extent during these seasons simply out of eagerness to nurse at any given opportunity.

In late summer, the season of heavy mosquito densities which probably harassed the grizzly family, distances between sow and cubs and between cubs increased dramatically. This dividing and spreading could have been a direct attempt to split up and thus reduce the hordes of mosquitoes that followed any one bear. Clouds of mosquitoes probably followed the family as they did myself. The spreading out of family members could have also been an indirect result of the sow feeding and moving about at a fast pace in highly erratic patterns, again probably to reduce mosquito harassment.

In early fall, with the mosquito season over, average distances between family members while active decreased substantially with distances between the cubs decreasing to about half of late summer distances. Movements of family members decreased slightly in early fall and may have contributed to the reduced distance between them. Movements remained higher than in spring and early summer due to greatly increased hunting of ground squirrels. Nursing halted or was severely reduced about a week and a half into this season and probably ceased to be a factor in maintaining proximity of the cubs to the sow. Movements also increased substantially around the time nursing ceased. Average distances

between sow and cubs while active were about 240% greater in the portion of early fall following the end of nursing than in the portion of early fall prior to the end of nursing. Distances between the cubs increased only 25%, suggesting that nursing may have played an role in maintaining very close sow-cub distances. Proximities prior to cessation of nursing are very similar to those of spring and early summer.

In late fall, distances between the sow and cubs increased to their highest seasonal level while distances between cubs, while increasing, remained well below their late summer highs. Movement by the family members increased to their highest levels as the sow spent even greater amounts of time hunting ground squirrels. This appeared to be the most important factor in the increased distances between family members, especially between the sow and cubs. Absence of nursing may have also contributed to the far greater increase in distance between sow and cubs compared with the increase in distance between cubs.

Travel and Proximity During the Recovery Period

During the period of the sow's recovery from handling the cubs spent more time traveling to the sow to check on her and sometimes rest beside her and more time was spent independently traveling to feeding sites and moving to and from resting sites. Active and resting distances from the sow at this time were at their highest average levels (Table 11). Cub 2 was also noted to become much more independent of the sow and cub 1, foraging around independently in much the same way as the sow normally did. Suprisingly, cub 2 spent no time at all during this period traveling to cub 1 to maintain proximity and little, if any, of

cub 2's feeding behavior at this time appeared to be oriented solely toward maintaining proximity to cub 1. Cub 1 on the other hand shifted his previous proximity - maintaining behavior from the sow to cub 2. Cub 1 oriented his feeding activity around cub 2 as cub 2 moved around and fed and cub 1 remained near her except for occasional trips back to the sow. Cub 1 also spent more time traveling toward cub 2 during this time then he was observed to do during the entire remainder of the year. This 'cub 2 leader' - 'cub 1 follower' relationship which temporarily arose between the cubs is suprising since cub 1 was larger, was probably stronger, was more aggressive and was a more effective forager overall than cub 2, especially in the late spring when cub 2 appeared to be in poorer condition than cub 1. The reasons for this are unclear. Possibly since cub 2 was female and cub 1 male, some instinctive maternal predesposition to lead her family, as the sow did, prompted cub 2's leadership role.

The behavioral changes noted in the cubs while the sow was largely incapacitated, such as their increased independence and the assumption of the leading role by one of the cubs, also provides insight into behavioral modifications which probably occur in grizzly bear young when the sow becomes severely ill or injured, or dies. Such behavioral modifications probably help the young to survive. Independence of action would become increasingly important to the survival of the cubs the longer the sow was incapacitated, and would be essential if she died. Assumption of the lead by one cub and following by the other cub would also facilitate their ability to move about together and forage extensively in a directed manner under a single leadership, and possibly enhance survivability.

Hourly Movements

Table 12 tabulates hourly average point-to-point movements by each family member for hourly periods in which:

1. A bear's active behaviors (excluding nursing) and unknown behaviors were less than or equal to 10% (6 minutes) of the previous hour's activity (i.e., nearly all resting).
2. A bear's active behaviors (excluding nursing) and unknown behaviors were greater than 10% of the previous hour's activity (i.e., largely active and mixed hours).
3. A bear's behavior during the previous hour was any combination of the above two categories (i.e., all hours combined).
4. A bear's active behavior (including nursing) constituted 90% or more of the previous hour's activity (i.e., nearly entirely active).

These movements are tabulated seasonally and yearly and also for the recovery period. Little movement occurred during hours that were mostly resting but once active (and unknown) behaviors became greater than 10%, movement became quite substantial.

Average point-to-point movements during hourly periods composed largely ($\geq$ 90%) of resting showed little change for all family members and point-to-point movements remained on the average less than 3 meters, during all seasons. Average point-to-point movements during hourly periods with substantial active components (> 10% or $\geq$ 90%) increased from spring to early summer, increased from early summer to late summer, remained about the same or slightly declined from late summer to early fall and increased again in late fall.

Table 12. Average movements (meters) from point to point on the hour.

| | Overall Hourly Average Movements | | | Average Movements w/Active Behaviors (including nursing) ≥ 90% | | | Average Movements w/Active Behaviors (excluding nursing) or Unk. Behaviors > 10% | | | Average Movements w/Active Behaviors (excluding nursing) or Unk. Behaviors ≤ 10% | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sow | Cub 1 | Cub 2 | Sow | Cub 1 | Cub 2 | Sow | Cub 1 | Cub 2 | Sow | Cub 1 | Cub 2 |
| Recovery Period | 59 | 77 | 81 | - | 158[1] | 140[1] | 176[2] | 109 | 110 | 7 | * | * |
| Spring† | 74[2] | 76[2] | 78[2] | 85[1] | 85[1] | 94[1] | 93[2] | 85[2] | 103[2] | * | * | * |
| Early Summer | 121 | 121 | 121 | 240[2] | 217[2] | 218[2] | 157 | 149 | 152 | * | * | * |
| Late Summer | 225 | 223 | 223 | 305 | 333 | 333 | 262 | 261 | 260 | * | * | * |
| Early Fall | 230 | 222 | 222 | 291 | 271 | 276 | 277 | 264 | 271 | * | * | * |
| Late Fall | 300[2] | 300[2] | 300[2] | 373[1] | 302[1] | 488[1] | 333[1] | 333[1] | 333[1] | * | * | * |
| Entire Active Year† | 188 | 184 | 184 | 278 | 266 | 284 | 228 | 218 | 224 | * | * | * |
| First 1/3 Early Fall† | 91 | 91 | 91 | 175[2] | 152[2] | 158[2] | 127[2] | 132[2] | 132[2] | * | * | * |
| Last 2/3 Early Fall‡ | 308 | 297 | 297 | 335 | 316 | 315 | 334 | 319 | 332 | * | 10[1] | 7[1] |

*Movements ≤ 3 meters.
†Excluding the recovery period.
†Prior to cessation of nursing activity (8/9 - 8/18).
‡Following cessation of nursing activity (8/21 - 9/8).
[1]Sample size < 10.
[2]Sample size ≤ 29.

A slightly different pattern emerges if early fall is divided into the periods before and after the end of nursing. Early fall movements before the cessation of nursing are less than in late summer (at the peak of the mosquito season) and similar to or somewhat lower than observed in early summer. Movements occurring in the period of early fall following cessation of nursing are substantially greater and are in fact about as high as values occurring in late fall. The availability and abundance of rich food sources at this time and the need to increase bodily reserves for hibernation apparently resulted in a greatly intensified search for food by the sow which substantially increased family movements.

Point-to-point movement during hours when a family member was active most ($\geq$ 90%) of the time ranged over the year from an average of around 90 m (300 ft) per hour in the spring to around 370 m (1,200 ft) per hour in the late fall. Again, these and all averages tabulated in Table 12 are minimum averages since the point-to-point movements recorded here are equivalent to taking a picture on the hour and another at the following hour and comparing the straight line distance between the 2. Considerably more movement than this usually did occur unless a bear was resting during most of the hour. Feeding movements consisted largely of several patterns of circuitous wanderings. At times the sow fed along a relatively straight path and then back along a parallel line. At still other times the sow fed while moving in what appeared to be an almost totally random pattern (as frequently occurred in late summer) and at still other times she fed while moving in overall single-direction patterns. Usually when feeding along a line, another smaller

pattern of highly erratic feeding movements occurred within the overall pattern. (Travel movements on the other hand always appeared highly directed with relatively straight lines of travel which did not have additional patterns superimposed thereon).

I estimate conservatively that actual total hourly movements, during hours when the bears were active most of the time, were roughly 4 times as great as the average hourly point-to-point movements shown in Table 13 (when the family was active at least 90% of the time). If accurate, average actual hourly movements, during hours where mostly active behaviors occurred, would have ranged from an average low of about 360 m (1,200 ft) in the spring season to an average high of about 1,500 m (4,900 ft) during the late fall season.

## DISTURBANCES

Disturbances are abrupt changes in the bear's behavior clearly resulting from outside influence. Disturbances were mostly of human origin though some were caused by other bears.

### Aircraft

Aircraft activity in the vicinity of the sow and cubs was the most common form of disturbance to the family unit. Of 18 observed instances where aircraft were in the area (11 helicopter, 7 plane) the sow showed no visible reaction in 4 instances (22%), a slight reaction in 7 instances (39%), a moderate reaction in 3 instances (17%), and a intense reaction in 4 instances (22%). A reaction was considered slight if the sow's reaction ranged from looking up at it to getting up and looking around for it. A reaction was considered moderate if the sow was disturbed enough by the aircraft to start walking away from it or started walking toward a place of better cover. A reaction was considered severe if the sow ran from the aircraft. Usually the sow showed either no reaction or only a slight reaction if aircraft was a half kilometer (1/3 mile) away or more, the sow probably being habituated to the noise of aircraft traffic in the area. The most notable exceptions occurred soon after the sow was first chased and immobilized via a helicopter and a transmitter surgically implanted in her neck. The sow appeared quite sensitive to aircraft for at least 10 days after this - reacting to the first aircraft observed in the area, at a distance of 0.5 to 0.8 km (1/3 to 1/2 mile) by running from it and to the next 2 succeeding aircraft that she was aware of by successively more moderate reactions.

Excluding the period following immobilization(s), approaches by aircraft to distances within roughly 90 to 540 m (300 to 1760 ft) of the sow typically caused slight to moderate responses in the sow. Approaches by aircraft to within less than 90 m of the sow usually resulted in severe reactions. (Similar severe reactions to the close approach of aircraft have also been observed in grizzly bears in Northeastern Alaska by Quimby, 1974.) The noise level of approaching aircraft appeared to be the key factor determining the level of disturbance to the sow; probably being joined by visual cues at close distances. This was illustrated in the extreme when a large unusually loud helicopter, which created a tremendous racket when it was still 3 kilometers (2 miles) away, coincidentally approached the sow and cubs and caused them to start running at a distance of well over half a kilometer (1/3 of a mile) - a distance at which light aircraft usually elicited no or only a slight reaction. Deliberate 'buzzing' of the sow, which also created extremely high noise levels and provided strong visual stimuli as well (as occurred when attempts were made to immobilize her) invariably resulted in severe reactions.

The cubs appeared largely unconcerned about the approach of aircraft and if they showed any visible reaction at all they were only mildly curious, or mildly nervous. If the sow's response to an aircraft was moderate and she started moving off, the cubs would follow, but they appeared unconcerned with the aircraft and only concerned about staying in the vicinity of the sow. Only when the sow's reaction was severe would the cubs react appreciably and then they would run with the sow. Association of the sow's fear reactions with particular environmental

stimuli probably served as learning experiences for the cubs on what stimuli in their environment should be avoided.

Human Presence

The remaining human disturbances occurred as a direct result of the observers in this study. On one occasion the sow chose the talus ledge directly below the ledge used by the observers and was startled by the approach of the relief observer. Though no additional noise was made the sow got up and moved 20 ft toward the observers looking in their direction, urinated, and remained standing listening and scenting the air for about 8 minutes before resuming resting. The cubs also halted their play when the sow got up and stood waiting for 5 minutes before resuming their play. On another occasion the sow, who was feeding along the base of the mountain, appeared to spot the observers who were standing on a talus ledge near the top of the mountain. She shortly moved from view. When she reappeared, she was standing on the ledge directly below, about 100 to 120 m (350 to 400 ft) away, with both cubs beside her. She was looking in the direction of the observers and stood on her hind legs twice trying to see and smell us better. She than ran off with her cubs back down the mountain and continued to run for about half a kilometer (1500 ft). She and her cubs then fed, grazing westerly until out of sight. The remaining occasion took place while I was traveling back to the main base camp and spotted the sow. The sow had also detected me but was not disturbed until my movements put me in a position in which my scent was carried to her by the wind and she identified me. At that point she ran off a short way. The sow appeared to be acutely

sensitive to human presence and in all observed encounters with humans, she reacted severely to their presence.

Other Bears

The only moderate to severe disturbances observed that were not of human origin resulted from actions by the cubs or by other bears outside the family unit. On at least several occasions either cub 1 or cub 2, through over-aggressive attempts to nurse or play clearly caused moderate disturbances of the sow which resulted in her getting up and walking off. On 3 other occasions the sow was moderately to severely disturbed by a 5 1/2 year old subadult male (possibly a offspring from her previous litter) who fed too closely; twice the sow intimidated him into moving off by walking toward him and once she ran off as he walked toward her. The cubs accompanied the sow on all 3 occasions. The most severe disturbance of the sow and her cubs occurred when they were disturbed while feeding on a caribou carcass by the approach of, and then the long pursuit by, a large adult boar grizzly. These interactions of the sow and cubs with bears outside the family unit are discussed in more detail in the section on intraspecific interactions.

## MOSQUITO HARASSMENT

Mosquito density as used here was considered high when clouds of mosquitoes of about 100 to 200 in number formed around the observer. Rough estimates of mosquito numbers were recorded on the hour when mosquitoes were present.

The mosquito season in the study area during 1977 stretched from about 10 June to 10 August. High densities of mosquitoes under favorable weather conditions occurred from the end of June through most of July, peaking in mid-July. Mosquito densities varied considerably according to wind and temperature. Recorded data indicated that the higher the temperature and the lower the wind velocity, the greater the density of the cloud that formed. Clouds of mosquitoes of about 100 to 200 in number, sufficient to require a headnet to prevent inhalation, accumulated in July when temperatures in the shade reached about 8°C (46°F) or higher, if wind speed remained 10 mph or less. Temperatures throughout the day exceeded this on most days in July, and mosquito density was generally largely dependent on wind speed.

During mid-July when the sow and cubs were under observation, changes were observed in their behavior which appeared to correspond with mosquito harassment. The sow's feeding pattern was dramatically altered at this time and became a rapid walk with highly erratic changes in direction. Time spent in any stationary feeding activity was substantially reduced. Ground squirrels were dug less and nursing of the cubs was sharply curtailed. The cubs occasionally would break into a run which appeared to be unrelated to play. The few rapidly disappearing snow banks along north facing creek beds, which were relative havens

from mosquito attacks, were sought out as resting places. Krementz (1888), as cited by Meyer-Holzapfel (1957) notes mosquitoes to be extremely hard on bears in marshy areas.

Somewhat similar behavior has been observed in caribou as a result of mosquito harassment in July at Prudhoe Bay, Alaska (White et al., 1975) and in reindeer in Norway (Thomson, 1977). With increasing levels of insect harassment caribou and reindeer spent more time moving about and they moved quicker with increasingly frequent outbursts of running. Insect harassment was noted to have been a major influence on the activity patterns of these ungulates and could substantially reduce the time spent feeding. Snowfields, gravel bars and other areas offering relief were sought.

Behaviors comparable to those of the highest levels of harassment of caribou and reindeer, in which considerable energy is expended trotting or running to escape, were not observed for the sow and yearlings. This may have been due to a different interspecific reaction. Direct comparisons between degrees of harassment of caribou and the grizzly family under the same conditions could not be made since by July caribou had left the study area.

While the mosquito harassment appeared to influence the sow's behavior substantially, the observed influence of mosquito harassment on the sow could have been somewhat greater than normal for other reasons. The sow had a transmitter surgically implanted in the back of her neck when she was immobilized on 29 May and the back of her neck was shaved for the surgery. There was no hair regrowth when she was again immobilized on 24 June but the area was covered with a regrowth of hair by

8 August. It is not known when sufficient regrowth occurred to provide protection from mosquitos and it is possible that the sow could have been more harassed than she would normally have been. As is the case with other grizzly sows the sow's facial area and portions of the underbelly around the mammae also were sparsely furred and nose and nipples were totally exposed. It seems certain therefore that while a bare patch on the back of her neck could have contributed to her discomfort, the sow's reactions could not be solely attributable to it. Discomfort may have also resulted from inhalation of mosquitoes when the sow stopped for any length of time during days of heavy harassment.

## AGGRESSION

### Methods

Aggression was defined as any threat or violence directed at another bear. Threat activity involved communication of intent to inflict pain or injury if a desired response was not elicited. Violent activity involved actual physical attacks by one bear on another apparently in an attempt to obtain a desired response and/or as a release of hostility.

In computing the frequencies of attack the period in which the sow was drugged and recovering from surgery was excluded from computations for the sow and included in computations for the cubs as a whole.

### Results and Discussion

Aggressive interactions discussed herein involve only those occurring within the family unit. Observations of aggressive interactions within intact bear families, either captive or wild, appear to be unique to this study. Studies have been made elsewhere involving aggression between adult grizzlies competing for food resources on a salmon stream (Stonorov, 1972; Stonorov and Stokes, 1974; Egbert and Stokes, 1976). These studies and studies of orphaned black bear young in captivity (Burghardt and Burghardt, 1974; Henry and Herrero, 1974; Pruitt, 1974, 1976; Jordan, 1976), have identified a variety of behaviors characteristic of aggression in black bears and brown bears: specific vocalizations, ear positions, facial expressions, head orientation, body orientations and motor patterns. In this study, because of the distance of observation and because of the extreme speed and shortness of duration of aggressive behavior involving attacks, only the more overt aggressive behaviors

were readily identifiable. Ear positions and facial expressions were not identified and only generalized descriptions of body orientations and motor patterns were made.

Threat

Only one overt threat incident was observed within the family group. One cub was checking out a ground squirrel hole the sow had just abandoned and the other was standing behind and to the side approximately 4 to 5 m (15 ft) away. The cub to the rear was in a stiff legged position with head down (below horizontal) and body oriented toward the other cub. One cub, probably the cub in the rear, was emitting loud bawls. This behavior was similar to that observed during aggressive encounters in black bear cubs (Pruitt 1976). Threat behavior was difficult to clearly identify except when it occurred during such close observations. Other observations made of cub 1 at a ground squirrel hole with cub 2 standing behind and off to one side may have been threat but not identified as such because distance obscured visual and auditory cues. Similar threats may have occurred during nursing. Threat behavior probably was associated primarily with prized food sources.

Attacks - Occurrences & Duration

Sixteen separate incidents of attack behavior were observed. Four involved the sow, 15 cub 1, and 14 cub 2. Attacks were characterized by the intensity of bites and swipes, by the extreme speed of movements and by the shortness of duration. Attack movements involved bites and/or swipes either singly or in combination and the lightning-like rapidity

of these movements made them nearly a blur. Attacks ranged from 1 to 12 seconds in duration and averaged about 5 seconds. This is considerably shorter than observed by Pruitt (1974) in experimentally induced aggression in orphaned black bear young, where physical contact averaged 29 seconds. Attacks may have been shorter here as a result of influence by the sow.

Attacks - Causation

Attacks were associated primarily with limited readily defendable prized food resources: ground squirrels for the sow and squirrels plus nursing opportunity for the cubs. Of the 4 attacks involving the sow, 2 involved ground squirrels and 2 involved over-aggressive behavior by the cubs. Of the 15 attacks involving cub 1, 12 (80%) were definitely related to prize food sources, as follows: nursing, 5; ground squirrels, 6; caribou carcass, 1. Of 2 doubtful incidents, both may have been related to nursing indirectly and/or to a preferred resting position. The 1 attack clearly unrelated to food involved an over-aggressive play attempt with the sow. Of the 14 attacks involving cub 2, 12 (86%) were definitely related to prized foods as follows: nursing, 5; over-aggressive nursing attempt, 1; ground squirrels, 5; caribou carcass, 1. Of 2 doubtful incidents, both may have been related to nursing indirectly and/or to a preferred resting position.

Twelve attacks occurred entirely between cubs. They involved nursing (5; 42%) ground squirrels (4; 33%) and a caribou carcass (1; 8%). Two (17%) were questionable. Of the 5 incidents involving nursing, 1 was directly related to an attempt by cub 1 during nursing to reach

across and nurse in cub 2's territory and resulted in what appeared to be a mutual attack. Cub 1 had been anxiously moving back and forth between mammae in his own territory, possibly having depleted his own supply of milk, while cub 2 was suckling steadily on the upper pectoral mammae in her own territory. Suddenly, cub 1 attempted to move in on cub 2's territory and they snarled and attacked each other. Three other attacks occurring during nursing appeared to involve either attempts by cub 1 to drive cub 2 from cub 2's nursing territory, or were explosions of rage by cub 1 due to depletion or near depletion of cub 1's milk supply. It was not possible to distinguish the primary motivation. The remaining one occurred when each of the cubs happened to be on the wrong side of the sow (the side opposite their own nursing territory) when the sow initiated nursing. These aggressive attacks between the cubs resulted in the sow terminating nursing or her offer to nurse in 3 of these 5 instances. It is likely the sow did this either to remove the source of aggression between the cubs to halt the conflict and/or because she was disturbed by the conflict. In other instances which were observed, the sow's behavior suggested concern during attacks between the cubs.

Of the 4 attacks involving ground squirrels, 1 occurred while the cubs were lying side by side, 1 m (2-3 ft) away from the sow, who was digging out a ground squirrel burrow, and resulted in cub 1 moving off. Apparently the cubs' relaxed resting position was transformed into a high-tension, keenly competitive position as the cub(s) recognized the imminent possibility of capturing ground squirrels escaping from the burrow. A second incident occurred immediately after the sow left a

ground squirrel hole which the cubs had been watching her dig and the conflict appeared to be over who would be first to check the hole for ground squirrels or scraps. In the third, cub 1 continued digging at a ground squirrel burrow that had been extensively dug by the sow, and cub 2 appeared to have moved too close to cub 1 while he was digging and cub 1 attacked cub 2, who retaliated in kind. The sow, digging for ground squirrels at an adjacent hole, turned around and moved between them and the fighting stopped. In the fourth, cub 1 started digging at a ground squirrel hole on his own and cub 2 again possibly approached too closely and cub 1 leaped on and attacked cub 2. Afterward cub 1 resumed digging ground squirrels and cub 2 resumed watching a few feet behind.

In the single incident involving a caribou carcass, cub 1 was feeding on the main portion of the well consumed remains. Cub 2 got up from resting and started wandering about, browsing and/or searching for scraps. Apparently cub 2 wished to feed on the main portion of the carcass but was hesitant to do so with cub 1 already there. After about 5 minutes however cub 2 went over to the carcass and started to feed. Cub 1 abruptly attacked cub 2 walloping her several times with his paws. Cub 2 backed away from cub 1, who resumed feeding and then cub 2 hesitantly returned to the carcass and also fed without incident. Interestingly, the sow, who was resting, had looked up and watched the aggressive interaction and then got up and moved closer to the cubs and carcass before resuming resting. This action by the sow may have been intended to intimidate the cubs from further aggression or to reduce the distance between her and the cubs so that she would be able to intervene (as she appeared to do in a previously noted incident) in case aggression resumed.

It would be interesting to know to what degree, if any, the sow used vocalizations to discourage or possibly halt fighting between the young.

Both questionable incidents that occurred may have been related indirectly to nursing or to a preferred resting position. In the first instance the sow had ended nursing by turning over on her side. Cub 1 came around to the other side where cub 2 was and appeared to be looking for an opening to squeeze in and nurse. As he moved in close to cub 2, who was now resting nestled against the sow in the abdominal region by her near leg, cub 2 attacked cub 1 with a flurry of hard, slapping punches. Cub 1 threw a few in return, backing off. He then gave up and moved to the anterior end of the sow and rested. In the second instance the sow was on her side resting and the cubs were resting nestled snugly against the sows body protected by the sow from a cold, stiff breeze. Cub 2 was resting nestled nearest the pectoral mammae and cub 1 nearest the pelvic mammae. Cub 1 got up and nestled in even closer. Cub 2 shifted her head closer to cub 1, apparently trying to find a more comfortable position. Cub 1 promptly nipped cub 2 aggressively, fast and hard. Cub 2 then moved her head away and tried to find a more comfortable spot on the sow in the other direction. The sow, however, looked at the cubs, got up and moved away and started browsing. The reason for this attack could have been because they might have recently nursed and as a result cub 1 may have been protective of his position, as may have been the case in the former instance when cub 2 attacked cub 1. Though no other competition was noticed for resting positions against the sow it is possible these last 2 aggressive incidents could have been related to a defense of a favored resting position. The cub in each

instance was resting in the sow's abdominal region which was the softest, warmest position available for resting.

Attacks generally seemed spontaneous with no advance warning, but this may well have been due in most, or at least many, cases to distance obscuring body signals and sounds. On several occasions the attacked bear, cub 2, appeared to have been totally taken by surprise by the attacker, cub 1.

There is some similarity between the causations of aggressive attacks found in studies of captive orphaned black bear cubs and those found here. Burghardt and Burghardt (1974) noted that the first aggressive behavior seen in a developing pair of black bear cubs occurred during nursing (from a bottle) when, as their milk ran out, their 'purrs' of contentment changed to growls as they attacked each other. Pruitt (1974), who studied these same 2 black bear cubs, found that of all forms of naturally occurring (non-experimenter induced) aggression 27 episodes involved 'ear sucking,' 16 occurred during feeding, 2 occurred over human attention, 2 occurred over possession of an object, and 1 occurred in reaction to one of the cubs standing over the other. In this case the only similarity observed was that of aggression in relation to feeding. The ear sucking may however have been a form of displaced nursing since the orphaned cubs when older were no longer bottle nursed.

Egbert and Stokes (1976) noted that aggression decreased among older grizzlies sharing a salmon stream when salmon were plentiful and increased when they were not.

Attacks - Initiation, Interaction & Termination

The bear who first attacked the other in a attack interaction was recorded where it could be clearly determined. The sow was involved in 4 interactions with her cubs. One involved an aggressive scrambling, juggling tug-of-war with little or no actual fighting, over a ground squirrel. It involved all family members and the initiation of the general melee appeared to be mutual. In the other 3 incidents the sow was the initial attacker, but only after considerable provocation. In the first of these incidents, which involved play or a play attempt by cub 1, all 3 bears were resting when cub 1 got up and started smacking the sow's nose with his paws. The sow popped up and nipped cub 1 on his side near his shoulder and cub 1 backed off. About an hour and a half prior to this the sow had engaged in rough play with both cubs, and both cubs had slapped the sow's muzzle repeatedly in play. Apparently the timing chosen (while the sow was resting) and the lack of play invitation played an important role in the sow's reaction. No other incidents were observed where play attempts or overly rough play led to aggressive interaction between family members.

In the second of these incidents, which involved a nursing attempt by cub 2, cub 2 came up to the resting sow wishing to nurse, then pawed at the sow's back gently, and finally nipped her in the back. The sow turned extremely quickly, biting at and swiping with her forepaw at cub 2 as she turned, but then braking in mid-motion and changing the swipe into a pushing motion, halting the attack just before actually making contact; probably because as she turned she realized it was only one of her cubs. The swipe the sow halted was much more intense and powerful

then any other observed and if carried through might well have killed or severely injured the cub. In both of these first 2 incidents the cubs immediately backed off when the sow exploded and the sow walked away rapidly and appeared to be agitated for a short while thereafter. The remaining incident occurred when cub 1 stole a ground squirrel the sow had spent about 20 minutes digging out and was about to consume. As cub 1 ran off with it a short distance and started to consume it, the sow let out a tremendous roar, walking rapidly to the cub with mouth open and slapped him hard and fast. Cub 1 ran off again with the ground squirrel and this time the sow did not follow but remained standing there briefly and then wandered around cub 1 who was feeding on the ground squirrel, but ignored him, and finally moved off looking for another ground squirrel burrow.

Another incident was also observed on 5 September 1977 involving ground squirrels among members of a different family. A female with 2 cubs of the year was engaged in digging ground squirrels with the spring cubs by her watching. Suddenly a ground squirrel ran out and all 3 pursued it. The adult female caught it and the cubs rushed in to try and grab it. One of them succeeded and ran off with it hanging from its mouth. As the spring cub approached the female again, the female started to rush toward it and the cub ran away from her. The female did not pursue the cub and the cub ate the ground squirrel while the female and other spring cub fed on berries.

The yearlings, who were clearly subordinate to the sow in this study, were not observed to initiate an aggressive attack against the much more powerful sow or even to defend themselves by fighting back in

the several instances where the sow initiated the attack. In the 2 non-food related incidents the cubs backed off, appearing cowed and then remained unmoving. This behavior appeared to be a form of passive submission, as noted by Fox (1971) in canids, and may have served to reduce aggression in the sow and prevent further attack. In both instances, the sow immediately moved off. Details of one of these incidents included backing off a few steps, just out of reach of the sow's forepaws, 'freezing' in a leaning back position on all fours with rump posterior to the hind legs and shoulder well posterior to the front legs. The head was oriented toward the sow with the mouth closed and muzzle down. This posture was reminiscent of, but less exaggerated than the 'head lowered and neck extended horizontally (crouch)' position observed by Fox (1971) to be associated with submission in canids. The cub remained in this position until the sow moved off. Egbert and Stokes (1976) stated that submissive postures are lacking in brown bears and that the nearest analogous behavior is defensive threat. While this may be true of adults, this was not the case in the aggressive interactions noted above between the sow and cubs; less overt submissive behaviors were also noted during nursing attempts.

In the 2 food related incidents, involving ground squirrels, cub 1, who grabbed the prize in both cases, immediately ran off a short distance with it before feeding. While cub 1's initial actions in grabbing away the ground squirrels were certainly not submissive in nature the actions following do suggest a position subordinate to the sow since running off was an attempt to prevent further aggression interaction which might well have resulted in loss of his prize. Both backing away, noted

previously, and running away, noted here, have been found to indicate subordinance in aggressive interactions between adult grizzly bears (Stonorov and Stokes, 1974).

In aggressive attacks between the cubs identifying the initiator of the attack was more difficult then in sow-cub interactions, since these interactions often began abruptly without any observable warning. Of the 8 of 12 instances in which the initial attacker was known, cub 1 was the aggressor in 6, cub 2 was the aggressor in 1, and in 1 instance both appeared to attack each other at the same time. Aggressive attacks would frequently begin with one cub lunging or leaping at, or jumping on the other to close the distance and/or throw the opponent off balance and obtain a superior position, and then immediately begin slugging. On other occasions when the cubs were within easy reach of one another the aggressor would either jump on the opponent and start slugging or simply start slugging. Typically attacks were composed of hard, fast, slugging combinations using the forepaws or slugging combinations mixed with biting. In one instance, a single bite was used. The attacked cub, especially if taken totally or partially unaware and at a disadvantage, would sometimes slip out of the attack by rapidly backing away and assuming what appeared to be a defensive, ready position in case the attack was continued, which it invariably was not once the attacked cub had successfully backed away and disentangled itself.

While the backing away extrication, and assumption of a defensive ready position, was similar in some respects to the submissive behavior noted previously in non-food related aggressive interactions with the sow, it differed most noticably in that an attack intention was clearly

conveyed in the event of further attack by the other cub. No hint of such a threat was conveyed in the submissive posture or during other submissive behavior. Other differences noted were a very short backing off (just a few steps) followed by freezing in place in the case of the submissive posture versus a much longer backing away (perhaps 1.5 to 3 body lengths) and no such freezing in place in the case of defensive threat. The defensive ready or threat position seemed to be an overt position of immediate readiness and preparedness to fight if further aggression ensued. The attacked cub faced the other one warily, often initially in a half crouch and/or with forepaw raised.

Sometimes swipes were thrown by the defender while extricating himself. Once the attacked cub had successfully backed away and the cubs faced each other warily, then the initial attacker would turn and resume his previous activity (when still possible) and the attacked cub would either resume his previous activity without further incident or change to other non-aggressive behavior.

In the remainder of the encounters the attacked cub attacked in return and a brief fight ensued. Neither cub ever appeared to gain a serious advantage and both cubs would typically break off by backing away and separate facing each other. It was not clear in any fight encounter which cub initially broke off the fight or if the break off was mutual. Neither cub appeared to be the obvious victor in any fight but body language or vocalizations which might have indicated such could easily have been missed. After separating, the cubs would eye each other warily and then go about their business, either resuming their former activity (where possible) or one cub changing his previous behavior.

One peculiar exception to the usual pattern of break off of fights was noted. When on one occasion cub 1 had initially attacked cub 2 and cub 2 started to fight back, cub 1 immediately broke off the encounter and ran back around to his own side of the sow. It is unclear whether cub 1 was running away from cub 2 or running back to his nursing position in an attempt to resume nursing before the sow terminated it, which she did. Of the 12 attacks observed between the cubs, the attacked cub responded in 4 (33%) of the encounters by immediately backing away and in 6 (50%) of the encounters by retaliating in kind. Of the remaining 2 encounters, 1 involved a mutual attack and in 1 instance no details of the encounters were recorded.

Since it was not possible to identify the victor in these encounters based on observation of the encounters themselves, behavior patterns preceeding and succeeding encounters between the cubs were examined to determine whether the aggressive interaction appeared to have changed the behavior of one of the cubs in a way favorable to the opponent. If encounters were judged to be victorious based on a clearly favorable change in the subsequent feeding behavior of the opponent and judged to be draws if no such change in behavior occurred, cub 1 won 1 of these encounters and cub 2 won 3. The remainder were either draws or indeterminate.

Neither cub appeared overall to dominate in attack encounters. Although cub 1 predominated in initiating attacks, most encounters resulted in draws or were indeterminate in result, and of those in which a cub did win, cub 2 actually won more. Cub 1 was the initial aggressor in most of the attacks in which the initiator was known, was the larger

and apparently stronger of the 2 cubs, was the more effective forager, was more aggressive in initiating nursing bouts, was more aggressive in initiating play bouts and was often rougher and occasionally abusive in play. It is surprising, that cub 2, who seemed relatively passive compared to cub 1, was not only not readily intimidated into changing her behavior as a result of aggressive attacks by cub 1 but appeared quite able to hold her own in actual physical combat with him, and was at least as apt to deter cub 1's behavior as cub 1 was to deter cub 2's.

Attacks - Seasonal Causations

Attacks reflected the seasonal availability of prized defendable food sources of limited availability. Those high quality prized foods were the sow's milk, ground squirrels and on one occasion a caribou carcass. In the spring observed attacks were associated entirely with nursing. Unobserved aggressive interactions, particularly threat behavior, may also have occurred to a lesser extent, between cub 1 and cub 2 over roots. While not generally prized by family members, roots appeared to be the only abundant food source available at this time. Because of cub 2's poor, possibly semi-starved condition at this time, and the effort required to obtain roots despite their abundance, they may have seemed semi-prized to her when she did not have to expend large amounts of energy to dig them herself. It is noteworthy that the sow who could easily obtain abundant quantities of roots for herself never behaved aggressively toward cub 2; often letting cub 2 steal roots the sow had uncovered and frequently abandoning root mats she had overturned to cub 2 when cub 2 came over to them and attempted to feed on them. Cub 1

appeared to be in a position intermediate to cub 2 and the sow in that while in relatively good condition and considerably more efficient in obtaining roots then cub 2, was considerably less effective than the sow in obtaining them and had to work hard for them. Cub 1 was not observed to let cub 2 take roots he overturned or abandon root mats to her until he was through with them himself. Cub 2 would wait patiently until cub 1 was done with an overturned mat and had left it before approaching it and picking it over for additional roots. Possibly some missed threat behavior on the part of cub 1 and/or previous attacks by cub 1 caused cub 2 to wait.

In early summer a variety of easily obtainable vegetative food sources became available. The sow started digging out ground squirrels occasionally, some of which escaped to become prey for the cubs, and a caribou carcass was found; aggression shifted to encompass these items more heavily.

In late summer when the family group was observed during the peak of the mosquito season no aggression was observed, probably because the relative occurrence of prized foods available to the cubs dropped off considerably. Nursing fell off considerably at this time and the sow dug for ground squirrels less, apparently as a result of the clouds of mosquitoes which probably harassed them when they stopped for any length of time.

In early fall nursing appeared to cease early on, while the availability of ground squirrels, which the sow began to spend considerable time digging, increased substantially. Aggressive attacks associated with nursing were only observed in the early part of early fall while

those associated with ground squirrels occurred later on in early fall. Berries, which became available at this time and which are notoriously prized by bears, did not appear to be fought over. Although berries were not scarce in the study area, they were largely a small, highly dispersed food source and were not readily defendable. During the limited observations made in late fall when the only defendable prized food was ground squirrels, a single attack and the only clearly observed threat, was noted to involve this food source.

Attacks - Frequency

Frequency of aggression in hours per occurrence was examined seasonally and over the entire year. The sow was involved in an aggressive attack roughly every 66 hours over the entire year (excluding the period in which she was drugged and recovering from surgery), cub 1 every 20 hours and cub 2 every 21 hours. Aggressive attacks occurred within the family group every 19 hours. Attacks between cubs occurred every 24 hours. Pruitt (1976) notes the "latency to a second agonistic interaction was at least 10 to 24 hours" between black bear cubs and is similar to that observed here. Seasonally an attack between the cubs occurred every 13 hours in the spring, every 18 hours in the early summer, were not observed in late summer (when observations were made at the height of the mosquito season and little nursing or digging of ground squirrels by the sow was noted), occurred every 43 hours in the early fall, and every 12 hours in late fall. While the seasonal sample size is too small to draw conclusions, the higher frequency of aggressive attacks between the cubs in the spring and late fall may suggest that

aggression between them was heightened at these times by reduced food supplies. In the spring there was a scarcity of readily obtainable foods and the sow's milk was the only high quality food source available to the cubs. In the second half of late fall the growing season was over, green vegetation was unavailable, nursing appeared to have long since stopped, and deepening snow cover made movements more difficult and ripened berries less easy to obtain. Ground squirrels were the only defensible prized food source remaining in a steadily declining environmental situation.

Vocalizations

Vocalizations were heard accompaning several of the aggressive interactions. In the single instance involving threat between the cubs, a loud 'bawling' was heard. In 2 (17%) of the attacks between cubs, growling or snarling vocalizations were heard. Of the 4 aggressive interactions involving the sow and one or more cubs, 1 (25%) involved an exceptionally loud roar during an attack on cub 1. These observations provide only a crude estimate of the minimum percentage of vocalizations that are associated with aggressive attacks since all vocalizations which occurred were not heard.

Only one vocalization was heard that was not clearly associated with aggression but this instance was probably indirectly related to aggression. The sow had been unconscious or too drugged to get up for 26 hours following immobilization and surgery in the spring. A few times in the previous couple hours she had tried to sit up, possibly

trying to scent her cubs, and had collapsed on her back. Finally she managed to get up and walk slowly and with great effort toward her cubs. When within 90 to 120 m (300 to 400 ft) of them she moved her jaw up and down and made what sounded like a heavy breathing/whooshing sound, possibly similar to the threat 'huff' noted in black bears by Jordan (1976). This vocalization may have been a threat-danger-call to the cubs. The cubs immediately came running and the sow nursed them.

# PLAY

## Methods

Play events were recorded to the nearest minute. Events of less than 30 seconds were tabulated as to occurrence but assigned a zero time value. Play sequences with breaks of less than 30 seconds (during which other behaviors occurred) were counted as one continuous play event. Play sequences interupted by breaks of 30 seconds or more were considered to be 2 separate play events. Play sequences in which the play partner was changed were considered 2 separate play events unless frequent interchanges of partners took place during play sequences or unless all 3 family members were simultaneously engaged in play interactions with each other.

Breaks in play-fighting to run and catch up to the sow after which play fighting resumed were considered interruptions and were not considered to be mixed play-fighting and play-running. Only where running itself involved play aspects was it considered part of the play bout. Instances of running, in which it was questionable as to whether play was predominantly involved or whether the running was predominantly goal oriented - such as to catch up to the sow or to escape mosquito harassment - were excluded from tabulations. Particular difficulty occurred where solitary play, which consisted mostly of play running was involved. As a result this category of play was probably substantially underrepresented.

# Results and Discussion

## Introduction

Young bears are highly social animals with a well developed system of social communication. The methods of social communication are similar in many respects to those observed in the Canidae (Fox, 1971) from which the family Ursidae evolved during the late Oligocene or early Miocene. Ear positions, facial expressions, body postures, motor patterns, and vocalizations have all been found to be important in social communication among bears. Pruitt and Burghardt (1977) present a literature review of such communications observed in various species of bears.

Detailed analysis of play behaviors has occurred for orphaned black bear cubs studied in captivity (Henry and Herrero, 1974; Pruitt, 1974). These have used movie cameras and slow motion and frame-by-frame analysis to detail a variety of behavioral patterns associated with play. These include a specific range of ear positions, facial expressions, and motor patterns. In addition it has been found that play is characterized by a lack of vocalizations. Such a detailed analysis of behavioral patterns and social communications of play has not yet occurred for grizzly bear young.

In my study, details of communication such as ear positions, facial expressions, and vocalizations usually could not be identified readily due to the distances at which observations were made and the speed of interactions. Movie cameras to record the fast moving detailed sequence of events such as occurred in play (and even more so in aggression) would have helped greatly when conditions were favorable but were

not available due to lack of funding. The advantages of such detailed observations for a thorough understanding of social communication and behavioral interactions are obvious, as are the advantages of observing behavioral patterns in their natural setting with their naturally occurring expressions. Despite the lack of fine resolution considerable information was gathered on the overt behavioral interactions and motor patterns associated with play in the wild.

## Classification

Play was classified into categories based largely on those of Tembrock (1958) and Henry and Herrero (1974). Modifications were made to fit the range of behaviors observed for the family under study.

Solitary play. Play not involving another individual (i.e. solitary playful running, rolling, pawing the air, play with an inanimate object or play with a body part).

Social play. Play involving a partner. This is further divided into the following categories: Play-fighting - physical contact with a partner and largely composed of behavioral patterns similar to but modified from those occurring during aggressive interactions; Running-play - involving chasing of the partner or running with the partner, with little or no physical contact; Play-fighting and Running-play - play sequences involving combinations of intermixed play-fighting and play-running in any combination of sequences; Sexual play - involving physical contact with the partner and largely composed of behavioral patterns similar to but modified from those occurring during breeding interactions. Sexual play was not observed during this study.

Yearly Occurrences

Eight play events were observed to involve the sow and one or more of her cubs over the year. Cub 1, in turn, was involved in 121 play events and cub 2 in 119. Of those in which the sow was involved, 7 (88%) involved play-fighting and 1 (12%) involved a combination of play-fighting and running-play. Of those in which cub 1 was involved, 89 (74%) involved play-fighting, 20 (17%) involved a combination of play-fighting and running-play, 9 (7%) involved solitary play, and 3 (2%) involved purely running-play. Of those cub 2 was involved in 90 (76%) involved play-fighting, 20 (17%) involved a combination of play-fighting and running-play, 6 (5%) involved solitary play and 3 (3%) involved purely running-play.

Of the play events the sow was involved in 3 (38%) involved play with cub 1, 3 (38%) involved play with cub 2, and 2 (25%) involved play with both cubs together. Of those play events involving cub 1, 5 (4%) involved play with the sow, 107 (88%) involved play with cub 2, and 9 (7%) involved solitary play. Of the play events involving cub 2, 5 (4%) involved play with the sow, 107 (91%) involved play with cub 1 and 6 (5%) involved solitary play.

If play bouts solely between the cubs are examined and play bouts involving combinations of play-fighting and running-play are categorized into either play-fighting or running-play according to which type made up the majority (where known) of the play bout, a comparison can be made with percentages of play-fighting and running-play categories tabulated by Henry and Herrero (1974) in captive black bear young. They found that in play between young, play-fighting made up 84% of play behaviors,

locomotory-play, which involved running chase (and less frequently climbing chase) and seize-the-object, 14%, and sexual play 2%. For the grizzly young in this study play-fighting made up 93% (n = 97), running-play (no climbing-play or seize-the-object play was observed) 7% (n = 7), and sexual play was not observed. It is uncertain whether the larger percentage of play-fighting observed in the grizzly young is reflective of interspecific differences between black bears and grizzly bears or simply of individual variations in preference for certain types of play. Environmental influences certainly played a role. The grizzly cubs in the study area for instance could not engage in climbing-play because there were very few trees tall and strong enough to support climbing activity. The role of the environment in influencing play types is discussed in more detail in a later section. In any case, play-fighting, as is the case with black bear young, seems by far to be the single most important play activity engaged in by the grizzly bear young. The age and stage of development of the young may play a role in influencing the occurrence of sexual play.

Average Duration of Play Types

Play involving the sow and one or more cubs averaged 2.6 minutes and play solely between the cubs averaged 3.7 minutes. If play bouts involving the sow are not considered to be discrete bouts in each instance where the sow switched play between one cub and the other, her average duration would be 4.0 minutes. Play bouts ranged in length from as little as 10 seconds to as much as 28 minutes. Average duration of the various types of play events are tabulated for each family member in

Table 13 as are the seasonal average durations for all types of play combined.

In black bears, play bouts between cubs averaged approximately 1.0 minute with a range of 0.25 to 6.0 minutes (Pruitt, 1974). Pruitt observed 2 young, primarily as yearlings. Henry and Herrero (1974), who examined 3 cubs of the year at the Calgary Zoo in mid-summer, recorded average play bouts of 0.30 minutes. These averages for black bear cubs are much smaller than the 3.7 minutes observed here for the grizzly young in this study. A small part of this difference may be accounted for by captivity and unnatural distractions of the black bear young and differing methodologies, at least for those observed by Henry and Herrero at the Calgary Zoo.

Herrero (pers. comm.) stated that considerable distraction of the cubs occurred as a result of the zoo environment and this may well have shortened length of play sequences considerably. Pruitt's bear young, which were held captive in seminatural surroundings, were subject to occasional man made distractions which she felt might have shortened play at times (pers. comm.), but she did not feel these frequent enough to have much effect on average duration of play. Methods used to decide when a bout was terminated appear to have been the same in both Pruitt's and my study. In both studies, interruptions of 30 seconds or more were considered bout terminations and all interruptions in play of less than 30 seconds were considered temporary breaks within a play bout (although possibly some breaks may have involved behavioral terminations of play bouts in which play was resumed very quickly through reinitiation by 1 or both of the cubs). Since unnatural distractions appeared to have

Table 13. Average duration (minutes) of play bouts* for each family member.

| Type | Sow Average Duration (min) | n | Cub 1 Average Duration (min) | n | Cub 2 Average Duration (min) | n |
|---|---|---|---|---|---|---|
| Playfighting | | | | | | |
| All combined | 2.9 | 7 | 3.8 | 82 | 3.7 | 83 |
| Cub 1-Cub 2 | - | | 3.8 | 78 | 3.8 | 78 |
| Sow-Cub 1 | 3.5 | 2 | 3.5 | 2 | - | |
| Sow-Cub 2 | 1.0 | 3 | - | | 1.0 | 3 |
| Sow-Cub 1-Cub 2 | 5.0 | 2 | 5.0 | 2 | 5.0 | 2 |
| All sow-cub | 2.9 | 7 | 4.3 | 4 | 2.6 | 5 |
| Play fighting & running | | | | | | |
| All combined | 1.0 | 1 | 3.6 | 18 | 3.6 | 18 |
| Cub 1-Cub 2 | - | | 3.8 | 17 | 3.8 | 17 |
| Sow-Cub 1-Cub 2 | 1.0 | 1 | 1.0 | 1 | 1.0 | 1 |
| Play running+ | | | | | | |
| Cub 1-Cub 2 | - | | 2.0 | 2 | 2.0 | 2 |
| Solitary play+ | | | | | | |
| | - | | 3.3 | 9 | 0.8 | 6 |
| All types of play | | | | | | |
| | 2.6 | 8 | 3.7 | 111 | 3.5 | 109 |
| Seasonally | | | | | | |
| Spring | - | | 3.8 | 4 | - | |
| Early Summer | 2.8 | 6 | 3.8 | 69 | 3.7 | 69 |
| Late Summer | 3.0 | 1 | 4.4 | 20 | 4.7 | 18 |
| Early Fall | 1.0 | 1 | 2.4 | 16 | 2.2 | 17 |
| Late Fall | - | | 3.5 | 2 | 1.4 | 5 |

*For all bouts observed in their entirety.

+Sow was not observed to participate in this form of play.

played only a minor role in Pruitt's study and since methodologies were very similar, average duration of play in my grizzly young appear to have been substantially longer than has been observed in black bear young.

In my study, interruptions that appeared to be simply temporary breaks as opposed to terminations included momentary separations during play-fighting, breaks to catch up to the sow (with play immediately resuming upon so doing) and short halts caused by an outside disturbance (such as the sow walking by). The only type of interruption which might have involved termination, involved breaking off play and walking off, and sometimes feeding; behaviors normally associated with termination. Breaks of this type were noted to normally last 5-15 seconds and the play-fighting was promptly reinitiated by one or both cubs. Whether these interruptions were brief 'breathers' within a play bout or actual terminations is unclear. Breaks of this type were not frequent, however, and if they were considered to be terminations, and these bouts divided in 2, it would only lower the average duration very slightly. Natural interruptions noted by Pruitt (pers. comm.) in her ophaned cubs involved noises made by animals (such as snapping twigs) and birds in the surrounding environment. Her cubs appeared highly keyed to noises around them.

Pruitt (1974 and pers. comm.) indicated that when play occurred between black bear cubs it did not usually appear as a single occurrence but commonly occurred in bouts at 30 seconds to 5.0 minute intervals during the observation period. In comparison intervals between play were much greater for the grizzly young. Only during early summer when play was most frequent did a similar clustering of play bouts appear to

be the rule; 49% of play bouts occurred within 2 minutes of at least one other bout; 61% within 5 minutes of another bout and 70% within 10 minutes of another bout. During the remainder of the year clustering was rarely observed at all and play was much less frequent.

It appears then that in the young black bear, play bouts were much shorter but there was also a much shorter interval between bouts, while in the grizzly bear young, bouts were much longer but intervals between were longer also. The shorter interval in black bear young, however, may reflect their being well fed and in captivity while the grizzly young in this study had to devote substantial amounts of time foraging for themselves, so bouts may have been much less frequent than if ample concentrations of nutritious food had been readily available.

Troyer and Hensel (1969) noted that grizzly young observed by them on Kodiak Island would sometimes play-fight for hours at a time. The longest play bout observed in this study was slightly under a half hour. Longer bouts may be common on Kodiak (and possibly more frequent as well) as a result of the easy availability of rich concentrated food sources (i.e. spawning salmon and clustered berries) which may have allowed grizzlies there much more free time from foraging. Alteratively, breaks in play may have occured during the Kodiak study which were not noted since play behavior was only noted cursorily there, rather than examined systematically. This would have resulted in the appearence of very long bouts which may have actually been a series of clustered play bouts.

Frequencies of Play

Frequency of play was tabulated for each type of play engaged in by each family member both seasonally and yearly (Table 14). Only cub 1 was observed to engage in play in the spring and play activity was confined to solitary play. Cub 1's limited attempts to engage in social play with cub 2 were rejected at this time and cub 1 was not observed to attempt to engage the sow in play. Cub 2 appeared to be in poor physical condition in the spring and had no inclination to play.

Shortly after the beginning of early summer play began in earnest and play during this season reached its highest frequency. Play-fighting dominated and play-fighting between the cubs was over 6 times more frequent than all other groupings of play combined. The high level of play was probably due at least in part to the meeting of basic physiological energy needs which were starting to be met with the advent of the growing season (which corresponded to the beginning of early summer). A week into the season a positive energy balance was well established by the consumption of carcasses of a cow caribou and her calf. Bekoff (1972) theorized that play is more likely to occur after basic physiological needs are satisfied and the satisfaction of these needs probably played an important role in the substantially increased levels of play observed at this time. In addition to energy needs, other factors which probably contributed to the particularly high levels of play occurring in early summer may have been moderate temperatures (as opposed to a cold wet environment in the spring and relatively hot weather in late summer), and the very low levels of mosquito harassment until the end of June.

Table 14. Yearly and seasonal frequencies[†] of play for each family member.

| | Play Fighting Cub 1-Cub 2 | | Fighting/Running Cub 1-Cub 2 | | Play Running Cub 1-Cub 2 | | Play Fighting Sow-Cub 1 | | Play Fighting Sow-Cub 2 | | Play Sow-Cub 1&2 | | Solitary Play | | All Play Combined | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Occ/day | n | Occ/day | n | Occ/day | n | Occ/day | n | Occ/day | n | Occ/day | n | Occ/day | n | Occ/day | n |
| Cub 1 | | | | | | | | | | | | | | | | |
| Spring | - | | - | | - | | - | | - | | - | | 1.45 | 4 | 1.45 | 4 |
| Early Summer | 21.22 | 62 | 1.71 | 5 | - | | 0.68 | 2 | - | | 0.34 | 1 | 0.68 | 2 | 24.64 | 72 |
| Late Summer | 4.86 | 12 | 1.62 | 4 | 0.41 | 1 | - | | - | | 0.41 | 1 | 1.22 | 3 | 8.51 | 21 |
| Early Fall | 3.09 | 11 | 2.25 | 8 | - | | - | | - | | 0.28 | 1 | - | | 5.63 | 20 |
| Late Fall | - | | 3.95 | 2 | 3.95 | 2 | - | | - | | - | | - | | 7.90 | 4 |
| Entire Active Year | 6.96 | 85 | 1.56 | 19 | 0.25 | 3 | 0.16 | 2 | - | | 0.25 | 3 | 0.74 | 9 | 9.91 | 121 |
| Cub 2 | | | | | | | | | | | | | | | | |
| Spring | - | | - | | - | | - | | - | | - | | - | | - | |
| Early Summer | 20.94 | 62 | 1.68 | 5 | - | | - | | 1.01 | 3 | 0.34 | 1 | 0.34 | 1 | 24.21 | 72 |
| Late Summer | 4.82 | 12 | 1.61 | 4 | 0.40 | 1 | - | | - | | 0.40 | 1 | 0.40 | 1 | 7.63 | 19 |
| Early Fall | 3.03 | 11 | 2.20 | 8 | - | | - | | - | | 0.28 | 1 | 0.28 | 1 | 5.79 | 21 |
| Late Fall | - | | 3.97 | 2 | 3.97 | 2 | - | | - | | - | | 5.96 | 3* | 13.90 | 7 |
| Entire Active Year | 6.87 | 85 | 1.54 | 19 | 0.24 | 3 | - | | 0.24 | 3 | 0.24 | 3 | 0.49 | 6 | 9.62 | 119 |
| Sow | | | | | | | | | | | | | | | | |
| Spring | - | | - | | - | | - | | - | | - | | - | | - | |
| Early Summer | - | | - | | - | | 0.64 | 2 | 0.96 | 3 | 0.32 | 1 | - | | 1.93 | 6 |
| Late Summer | - | | - | | - | | - | | - | | 0.38 | 1 | - | | 0.38 | 1 |
| Early Fall | - | | - | | - | | - | | - | | 0.27 | 1 | - | | 0.27 | 1 |
| Late Fall | - | | - | | - | | - | | - | | - | | - | | - | |
| Entire Active Year[+] | - | | - | | - | | 0.18 | 2 | 0.27 | 3 | 0.27 | 3 | - | | 0.73 | 8 |

[†]Frequencies for each bear are based on total observed time for each bear and the number of observed occurrences. Slight differences in frequencies of social play may exist between bears involved due to the slightly different total observation times for each bear.

*All occurrences were less than 1/2 minute in duration.

[+]Yearly observation time for the sow excludes the period in the spring in which she was drugged and incapacitated.

In late summer the frequency of play dropped to roughly a third of that observed in early summer, largely due to a decrease in play-fighting between the cubs. Hot weather and mosquito harassment were probably contributing factors as was possibly the increased movement by the sow which required increased movements and attentiveness by the cubs. Play events with running-play components were sometimes partially directed toward decreasing proximity to the much more mobile sow and increased movements may have contributed somewhat to the maintenance of, or slight increase in, previous levels of running-play activity. One other factor that might have contributed to the decline in play was a possible decline in the quality of food sources. Caribou carrion was no longer available and the favorite (and probably the most nutritious) emerging new plant growth was becoming increasingly hard to find, even in late melting snow bank habitats.

In early fall overall frequency of play appeared to decrease slightly. Play with play-running aspects remained the same or increased slightly while play-fighting declined. High levels of movements by the sow continued during this time (though for different reasons) and probably had the same effects as in late summer. The increased proportion of time spent feeding in preparation for winter may have also been a factor.

In late fall observation time was small compared to other seasons so firm conclusions are difficult to draw. Play frequency may have remained at levels roughly similar to late summer and early fall. Cub 2's play frequency was substantially inflated by 3, 5- to 10-second instances of solitary running-play. Pure play-fighting, whose frequency had been declining seasonally, was no longer observed and play-fighting

mixed with play-running and pure play-running, appeared to increase substantially, and were codominant. Again high levels of movements by the sow, the highest levels of any season, may have been a contributing factor in the substantially increased levels of play with running-play components. The proportion of time spent feeding also increased further in late fall. Environmental conditions deteriorated steadily and increasing snow depth in the second half of late fall gradually hid food sources available to the cubs and hindered movements. Increasing snow depth may have also hindered rough and tumble play-fighting activity at this time.

Play between the sow and young was quite infrequent throughout the year compared with the amount of play which took place between the cubs. According to Murie (1981) the amount of play between a sow and young depends on the litter size; if a sow has only one cub a sow and cub will spend considerable time interacting in play, but if the sow has 2 or 3 young the cubs largely play among themselves. Troyer and Hensel (1969) in contrast note that sows "...often enter into play with the cubs, ...". Differences may again result from the great abundance of concentrated nutritious food sources on Kodiak which may have allowed considerably more free time to be devoted to play.

## Associated Activities

Activities preceding and succeeding play were examined to see whether play tended to be associated with particular activities. Activities associated with play were very similar for the cubs. For the family as a whole active behaviors made up 85% (n=167) of all behaviors immediately preceding play while resting behaviors made up only 15%

(n=29). Over the year active behaviors made up about 64% and resting 36% of all behaviors. This indicates a higher tendency for play behavior to succeed active periods than resting periods. Feeding, which composed most of all active behaviors, constituted 67% of preplay activity of the family. This again may lend support to the theory that play is more likely to occur after basic physiological needs are satisfied (Bekoff, 1972). Burghardt and Burghardt (1974) and Pruitt (1976) who observed the same two captive black bear young at different ages, found that play could be predicted after feeding periods. Egbert and Stokes (1976) noted that play in grizzlies increased with increasing salmon levels (while aggression decreased). It is also possible since feeding continued throughout most of the day the bears may have tended to be relatively satiated as to food needs at any given time if their food needs were being met. The association between activity and play then may have been due to the possibility that a active bear was more likely to start playing than a resting, perhaps somewhat lethargic, bear.

For the family as a whole active behaviors made up 86% of post play behaviors (and feeding 64%). This also indicates a strong tendency for the family to engage in active behaviors (again mostly feeding) following play, rather than resting. Perhaps a bear who has just engaged in play, (which generally appeared to be an intensely stimulating activity), and who was still somewhat aroused afterwards, may have been less likely to rest immediately afterwards. In any case, play was more associated with active behaviors. Burghardt and Burghardt (1974) note the opposite to be the case in black bear young (spring cubs) raised by him and states that after a play bout, a rest period would follow.

Initiation of Social Play

Difficulty was encountered in clearly identifying the initiator of most of the play bouts. This was due largely to distance, which obscured many subtle forms of communication of play intent, and at times to missing the initial interaction. Sometimes it was difficult to identify the initiator of play even though play bouts were considered to be initiated by the cub first using an overt motor pattern of initiation. For instance, play was at times clearly initiated by one cub walking toward the other and making direct eye contact with the other, but at a distance it was not usually possible to distinguish this from proximity-maintaining behavior between cubs. If one cub walked toward the second looking at it and the second 'pawed the air' (another play invitation gesture) was the cub 'walking toward' the other the initiator and the 'pawing the air' a response or was walking toward incidential and the cub who was pawing the air the initiator? Because of difficulties in identifying the initiator with a reasonable degree of certainty out of 107 social interactions between the cubs only in 39 instances was the initiator identified. Of these, cub 1 was the initiator in 64%: cub 1 initiated 67% of play-fighting bouts (n=30), 50% of mixed play-fighting and running-play bouts (n=8) and the single instance in which the initiator of running-play was known. Play between the sow and cubs was at one time or another initiated by each family member. Two of these were known to be initiated by cub 1, 1 of these by cub 2 and 1 by the sow.

Motor Patterns of Initiation of Social Play

A variety of motor patterns was identified to be used to initiate play between the cubs. Motor patterns noted in play-fighting between the cubs included a direct walking approach with what appeared to be eye contact with the other cub, a running approach, leaping at or pouncing on the other cub, running into the other cub, pawing the air while looking at the other cub from a standing position (on three legs), rolling on the side and pawing the air at the other cub and rolling on the back and pawing the air at the other cub. If the cubs were close enough for immediate contact initiation would take the form of direct bites (play nips), swats or pawing at (touching) the other cub, sometimes combined with a sudden lunge at the opponent. Sometimes bipedal rearing by both cubs was observed at the onset of a bout. At times, especially if the opponent was recumbent, the other cub would circle it and then leap at the opposing cub where its defense appeared weak. Cub 1 was noted to initiate 1 play bout with the sow by pouncing on her and cub 2 was noted to initiate 1 play bout with the sow by 'pawing the air' toward the sow while lying on her back. Pawing the air appeared to be a favorite type of initiation by cub 2 but was seldom used by cub 1. Cub 1 seemed to favor walking approaches, running approaches or lunging and 'leaping at' initiations and may reflect his more active role in initiating play-fight bouts. Biting was a favored initiation procedure for both cubs when in contact distance of one another.

Motor patterns of initiation noted in mixed play-fighting and play-running were similar to those motor patterns noted to initiate pure play-fighting at times when play-fighting was the initial type of

play. When play-running was the initial type of play, motor patterns of initiation usually involved 'running at' the other cub, who would then run away and be chased. 'Running away' from the other cub, and inviting a chase, was also observed. Perhaps the most unusual initiation of play occurred on one occasion when cub 1 was walking back toward cub 2. Cub 2 stopped when she saw cub 1 heading toward her, assumed a stiff legged posture and playfully hopped once toward cub 1. Cub 1 looked intently at cub 2 and then started running toward her. Cub 2 then ran off, chased by cub 1, and soon stopped, turned around and play-fighting began.

Only 3 of the 112 social play bouts involved only pure running-play. One involved cub 1 running at and chasing cub 2 and 2 appeared to involve nearly simultaneously begun play episodes consisting simply of running around together and not involving a chase.

Initiations of play-fighting appeared to be similar to that observed by Henry and Herrero (1974) in black bear young except that head butting was not noted here. This type of initiation may have occurred however, but could have been overlooked. In running-play in black bear, Henry and Herrero (1974) found play events to be initiated usually by one of the cubs walking up to the other from behind and play nipping that cub from behind. This was not noted here, at least not during running-play, and could be more uncommon among grizzly bear young than among black bear young. Or since different preferences seemed to exist for certain types of play initiation techniques even between the 2 grizzly cubs observed in this study, this may not have been one of the preferred techniques used by these individual cubs, without a species - specific

relationship. Henry and Herrero (1974) observed the 'running-at-chase' without initial physical contact, which I observed in the grizzly bear young, to occur in black bear young as a common chase initiation alternative to the 'sneak bite.' The 'chase invitation' initiation technique observed here, which was not common, was not noted for the black bear young.

Motor Patterns of Play-Fighting

A number of motor patterns were observed to occur in play interactions between the grizzly cubs and are described below. All observed patterns appear to be similar to those observed in black bear cubs (Henry and Herrero, 1974; Pruitt, 1974).

Play biting and biting attempts. This motor pattern involved the use of the jaws to bite or attempt to bite, and were usually conducted in a restrained fashion so as not to cause serious injury. Bites were largely directed toward the opponent's head area and often involved jaw wrestling as well. The head area appeared to be the most strategic place for orienting bites. The jaws were the most important and probably the most painful weapon used in play-fighting and if they could be maneuvered out of the way, would make the opponent vulnerable to a bite (and possibly a pin) without the attacking cub getting bitten itself. Bites were by no means restricted to the head area, however, and any vulnerable body part accessible might be bitten to advantage at times. Bites were noted to the head (muzzle area, cheeks, and ears) neck, shoulder, flank, rump, and feet.

Jaw wrestling. This motor pattern of play involved maneuvering of the head and in particular the jaws, in which the cubs interlocked jaws repeatedly, twisting muzzles around and apparently trying to throw each other off balance and gain an advantage; possibly also to gain a superior muzzle hold which would restrict the biting ability of the opponent while maintaining a painful controlling hold.

Body wrestling. This motor pattern consisted of arm movements generally aimed at pushing or pulling the opponent off balance in order to gain a advantage through momentary lapses in the opponent's defenses, or to momentarily push, hold, or pin the opponent's head in such a position as to allow a clear undefended attack, or to block or break attacks by the opponent's jaws or paws. Face pawing (sometimes involving restrained clawing as well) was often used in the initial engagement between the cubs and seemed to be used as a feint to feel out the opponent's defense and to help set up the attack. Lunging at the opponent frequently occurred during or after initial pawing.

Swatting. This category consisted of slapping punches, usually fast and vigorous using the bottom of the forepaw. Swatting was usually directly at opponent's head, neck and shoulder regions. Occasionally boxing matches appeared to develop and smacking the opponent appeared to be a goal in itself as was the deliverence of a good play bite. Boxing matches were frequently associated with bipedal rearing. On other more frequent occasions when swatting occurred during wrestling matches, it often appeared to be used to try to knock the opponent off balance to gain or regain an advantage in the match.

Kicking. Kicking consisted of using the hind feet in fast vigorous kicks at the opponent. This usually occurred on occasions when one cub was underneath the other who was standing (horizontally), frequently when one cub had gained a superior position and had obtained a skin bite hold on the other. The cub underneath would use both hind feet rapidly and alternately to attack the other cub much in the manner of playing kittens. Kicks were mostly directed toward the other cub's underbelly or face. Claws were sometimes used as well. Kicking could also occur when both cubs were lying play-fighting side by side on their sides, particularly when play became intense. Cub 2 seemed to favor this technique more than cub 1 (possibly because she was usually on the bottom) and learned to use it quite effectively at times against cub 1's attacks.

Lunging or leaping. This motor pattern involved springing suddenly forward toward the opponent or leaping at or on the opponent. It appeared to be oriented toward the shoulder region of the opponent and designed to get around frontal defenses and/or jar an opponent off balance to weaken the defense and facilitate attack.

Rolling. Rolling on one side was often used to shift wrestling matches to a lying on side position. Sometimes it appeared to be used to break an opponent's hold as well.

Rearing. Rearing consisted of standing on hind feet. Sometimes the cubs would begin play by rearing simultaneously or almost simultaneously. Sometimes rearing would occur after momentary breaks and separations in play. Both cubs would engage in slugging and/or biting and/or push-pull hold wrestling, often intermixing them in various

combinations. The goal appeared to be to knock the opponent off balance and gain an advantage. Bipedal rearing play-fighting commonly gave way to horizontal standing play-fighting and/or to fighting lying side by side.

Head shake. Head shake consisted of 1 cub grasping the opponent's skin and fur between its teeth and vigorously shaking its head back and forth, much like a dog worrying a bone. This usually appeared to occur at times when one cub had the other pinned in a highly vulnerable position. Cub 1 appeared to use the head shake more often and more vigorously than cub 2.

Play-fighting could occur in almost any position in which 1 or more paws could be freed from use in support, for the interaction. Standing vertically on hind legs (bipedal rearing), standing horizontally, sitting, lying on back, lying on abdomen, and lying on side were all used as were positions intermediate to these. Positions frequently changed repeatedly during a bout. Typically both cubs assumed the same general positional stance during a bout (i.e. both rearing, both standing, both lying). Sometimes, however, play would occur with 1 cub (usually cub 1) standing (horizontally) over the other cub who was on its side or back. Most time spent play-fighting appeared to occur in the lying positions. Body wrestling, jaw wrestling, biting, and swatting were the most common motor actions of play-fighting. Often all were noted to occur at least once during bouts though occasionally 1 or 2 of these patterns would be totally absent during a bout. Frequently 1 or 2 of these motor patterns would dominate during a match. Jaw wrestling appeared to be an especially important part of play-fighting in early

summer but seemed to decline in play-fighting in succeeding seasons.

Observations of motor patterns of interactions between sow and young were infrequent. Pawing, swatting, biting, lunging and pouncing on were observed to be used by the cubs in playing with the sow and actions were similar in scope to those used by the cubs in play between themselves. Positions assumed by the cubs during play included rearing, horizontal standing and lying. No jaw wrestling was observed and body wrestling by the cubs was limited to low-intensity pawing (and sometimes clawing) at the sow's face. Play-fighting consisted almost entirely of bites and swats and pawing at the sow's face. Jaw wrestling and body wrestling may have been largely ignored by the yearlings because such movements would have been ineffectual against the tremendously more massive and powerful sow. Motor patterns observed to be used by the sow in play with the cubs consisted of body wrestling, bites, swats, lunges, and head shakes. In a bout the sow would typically roll the cub over, pin it, bite its neck and usually administer a head shake and/or drag it a bit and then let it go, where upon it would frequently attack her face again and she would swat it or grab it by the neck and roll it over and pin it again and shake it and/or drag it. In 1 play bout, cub 2 was noted to repeatedly take advantage of cub 1 whenever the sow had him pinned and would rush in and bite his feet. During play with the cubs the sow remained standing (horizontally) throughout. Bites by the sow to the pinned cubs appeared to be identical to the intense neck bite hold noted at times, in play-fighting between black bear cubs (Henry and Herrero, 1974) and occasionally observed in play-fighting between the grizzly cubs. The play-fighting instances noted between the sow and

cubs here appear to be somewhat different than has been observed by Murie (1981) who in play between sow's and lone cubs observed play to consist chiefly of the cub 'tugging and grasping at the mother's head and neck while she paws gently at the cub.' Perhaps the differences are due to individual variations or perhaps Murie (1981) may have been describing sows with a spring cub who may have required somewhat gentler handling than the yearlings in this study. Here play between sow and yearlings tended to be considerably rougher. Head and neck orientations noted by Murie (1981) in play attacks by cubs on the sows were similar to the head orientation noted here.

Motor Patterns of Mixed Play-Fighting and Play-Running

In play bouts combining both play-fighting and play-running the motor patterns of each component part appeared largely the same as occurred in their 'pure' forms. Motor patterns of play-fighting observed here were the same as observed in play-fighting by itself. Motor patterns of the associated play-running, as the name suggests, consisted almost entirely of running behaviors. In all except one bout of play between the cubs in this category, running consisted of chase behavior in which one cub chased the other and in nearly half of these instances the chase alternated at least once between the cubs with the chaser later becoming the chased. Play could begin either with play-fighting or with play-running but tended to follow a seasonal pattern similar to the shift in play types.

One cub typically would chase the other one around and eventually either the other cub would turn around and play-fighting would commence,

or the chasing cub would catch up, often administering a play bite to the shoulder, or more usually the rump, and then the chased cub would turn around and play-fighting would commence. At times the chase would alternate between cubs without intervening play-fighting and shift when one caught up with the other; taking on the form of a game of tag.

Usually cub 2 appeared to be thoroughly involved in the play bouts, however, at times it appeared she wanted to terminate the bout but could not. Breaking away from a play-fighting encounter and running off was often used as a method of terminating play-fighting as well as a way of initiating running-play within a mixed play-fighting, running bout and when cub 2 wished to end such a bout it appeared she had difficulty getting cub 1 to allow her to do so. Cub 1 would repeatedly chase her around and would catch up to her and bite her whenever he felt like it and reinitiate play-fighting. Surprisingly, cub 2 was never observed to force the issue and no play bouts were observed to turn into agonistic encounters. Cub 2 would simply play-fight briefly and break off and run off again and this would often occur repeatedly. Frequently chases between the cubs would be oriented around or toward the sow and would also serve to maintain proximity to the sow as well.

One observed bout of mixed play-running involved both a chase and simply running around together for a period of time. A single instance of a mixed bout was observed involving the sow and cubs.

Motor Patterns of Running-Play

Of the 3 play events involving entirely running-play, 1 consisted of a running chase and 2 involved the cubs running around frolicking

together, either side by side or with one cub slightly in the lead. Play-running involving running together has not been noted in studies of black bear young. Henry and Herrero (1974) note only 2 forms of running-play to have been observed; chase as noted here, and seizing an object. Seizing an object in captive black bears consisted of stealing an object, such as a bone or branch, that was chewable but not usually edible, from the other cub and fleeing with it. The other cub, sometimes immediately, but more often after a few minutes, would then approach and steal it back. One such play attempt appeared to have been made by cub 1 in the spring but no response was elicited from cub 2 who had no inclination whatever to play during this period of time. Such play between the grizzly cubs appeared to be very uncommon.

Motor Patterns of Solitary Play

Solitary play was not observed for the sow and only 13 clear instances were observed for the cubs. Motor patterns observed were: solitary play-running, jumping, rolling around on the ground, pawing the ground, pawing the air, and playing with the other (unresponsive) cub. Play-running was a component of all except 1 solitary play event and was the sole motor action in 8 of these events. Play-running consisted of frisky energetic loping movements and often involved running in seemingly random directions or simply running around in circles. Repeated high bounding or jumping movements were noted during at least 1 play-running episode. Rolling vigorously around on the ground for a time occurred along with running around in circles in 1 play event and in another rolling was combined simultaneously with extensive pawing of the ground.

Pawing the air occurred on 1 occasion after cub 2 rolled on her back. She pawed the air with all 4 feet for 1 to 1.5 minutes. The remaining motor pattern, playing with the other cub, was included here rather than in social play because of the lack of interaction. In this event, which occurred in the spring when cub 2 was in poor condition and had no inclination to play, cub 1 was romping about engaging in solitary play-running. Cub 1 then ran into cub 2 (who was feeding) in a play attempt, and wrestled the unresisting cub 2 to the ground, pawing and nipping her for a minute while cub 2 played dead, lying on her side and not responding in the slightest. Cub 1 then resumed solitary play-running and later ran by, seized the root cub 2 was feeding on, and ran off with it, probably in an attempt to engage cub 2 in a 'seize the object' running-play. Cub 1 again resumed solitary play-running. Solitary play-running, in this instance, was at least in part, a substitute for social play which during spring was not provided by cub 1's normal partner, cub 2. It is likely that a large portion of cub 1's solitary play-running at this time was due to the fact that he had no play partner.

Solitary play-running was probably much more common then indicated in Table 15. Many more solitary running episodes were observed in which there was some question as to whether they were predominantly play or even partially play. These were excluded from tabulations. Many such short episodes ($< 30$ seconds) were not recorded while longer ones ($\geq 30$ seconds), of which there were many fewer, were placed in the miscellaneous category. It was particularly difficulty to distinguish play-running from nonplay-running during late summer when mosquito harassment was occurring.

Environment and Play

None of the solitary play motor patterns observed here for the grizzly bear young were noted to occur in solitary play observed by Pruitt (1974, 1976) in her study of play in captive black bear young. Solitary playrunning could have been inhibited in the black bear young by their enclosure in a small area (18.3 x 18.3 meters) but this is unlikely since running chase play normally occurred within this same enclosure. Possibly, however, a larger area was needed. Solitary play made up over a quarter of all play events recorded during Pruitt's (1974) study and all recorded events were made up of play with inanimate objects, typically with trees or small branches within the enclosure. Such play most often involved paw or mouth manipulations of the object. The grizzly bear yearlings in this study were not observed to play with inanimate objects though very small trees and branches were common along the larger creeks, and low lying woody shrubs were common over large portions of the study area. These differences appear to have been due both to the differing environments and lifestyles of the barren-ground grizzly bear compared with the forest dwelling black bear. The black bear uses trees for protection and sometimes extracts food such as nuts from branches and overturns logs for grubs. For the young black bear, maneuvering and familiarizing itself with common everyday objects in its environment through play is beneficial to learning about them and to becoming knowledgeable about its environment in general. Such objects are much less common on the North Slope and object play is much less important to barren-ground grizzly young. (Grizzly young in Denali Park, which presents mixed environments of pure forest, tall brush, and

pure open tundra, do engage in some object play. Murie [1980] notes that when tall willow brush is encountered, cubs "... often climb among the limbs or lie down and spar with overhanging branches."). Play-running on the other hand, is much more important to grizzly young. Wide open spaces provide greater opportunities for extended running-play and the development of motor skills of running also have more important survival value to them. Barren-ground grizzly young have no trees to climb for protection and all age classes of young as well as subadults and even adult females may be subject to predation by large adult boars. Grizzly bears are also more predatory than black bears and often rely on sudden bursts of speed to surprise and catch large prey. The mixtures of solitary play-running, social play-running and play-fighting reflect the environment of the barren-ground grizzly young and all appear to serve to enhance their survival, while in turn the mixtures of solitary play with small branches and trees, social climbing chases, running chases, seize the object, and play-fighting reflect the environment of the black bear young and all appear to serve to enhance their survival.

Eibl-Eibesfeldt (1970) and Beckoff (1972) indicate play in general to be characterized by the individual learning about its environment and developing motor skills that are useful to the animal in later life.

Motor Patterns of Social Play Termination

Play bouts typically were terminated when 1 cub, or occasionally both cubs, broke off and either walked or ran off (usually a short distance) ignoring the other cub and beginning some other activity. More rarely the cubs would simply remain in place. During play-fighting

52.8% ended in one or both cubs walking off; 41.7% in one or both cubs running off; and in 5.6% both cubs remained in place (usually resting by the sow). Cub 1 usually broke off play by walking off while cub 2 usually did so by running off. In play between cubs, termination of play bouts were roughly evenly divided between cubs (Table 15). In play consisting at least partially of running-play components the data, though limited, suggest that cub 2 terminated play much more frequently than cub 1. This may be due in large part to instances where cub 2 no longer wished to play and ran off, being reinitiated by cub 1 and turned into mixed play bouts which cub 2 eventually succeeded in terminating. Of the bouts involving the sow and one or more cubs the sow appeared to terminate most of them.

Unsuccessful Play Attempts

A number of play attempts by the cubs were observed in which the conspecific did not respond favorably and no play bout resulted. Of those between the cubs almost all failed attempts were initiated by cub 1 Most attempts involved motor patterns also observed to successfully initiate play; pawing at, swatting, sneaking up and nipping, and running at. More unusual methods were also noted. One such, which was noted previously, was seizing an object (a root) from the other cub and running off with it. Another was running into the other cub and running off again which appeared to be an attempt to get the other cub to chase it. Another unusual attempt involved one cub chasing the other and repeatedly, while both were running, catching up to the cub who did not want to play and bumping it with its shoulder. Another involved running into the

Table 15. Play termination between cubs.

| Terminator | Play Fighting | Play Fighting/ Play Running | Play Running | All Social Play |
|---|---|---|---|---|
| Cub 1 | 48% (n = 21) | 10% (n = 1) | - | 39% (n = 22) |
| Cub 2 | 34% (n = 15) | 80% (n = 8) | 100% (n = 2) | 45% (n = 25) |
| Mutual | 18% (n = 8) | 10% (n = 1) | - | 16% (n = 9) |

other and playing with the other cub as though play-fighting but with the other cub lying limp and unresponsive. On one other occasion a cub appeared to use an exaggerated looking-away action with head tilted to the side and shoulder exposed and oriented toward the other cub. It was similar to a form of play solicitation among canids described by Fox (1971).

Motor responses of the cub rebuffing play attempts included ignoring the other cub, avoiding and then ignoring the other cub and using what may have been an open mouth threat gape similar to that described during aggressive threat between cubs by Henry and Herrero (1974). It is difficult to be certain it was a threat gape however, since in its gross aspects the threat gape appears identical to the play face. Since, however, cub 1 broke off his play attempts when this occurred, it probably did involve the threat gape rather than play intention on cub 2's part.

Of the 4 observed unsuccessful play attempts by the cubs with the sow, motor patterns included pawing at the sow's face, pawing at and clawing at the sow's face, pawing the sow's muzzle and gently nipping her face, and very vigorously and repeatedly swatting the sow's nose and muzzle hard. In the first instance the sow simply ignored the cub, in the second she walked off, in the third she pawed at the cub once and then ignored it. In the last instance, which occurred while she was resting, the sow reacted aggressively, jumping up, nipping the cub, and then walking off.

## MISCELLANEOUS ACTIVITY

Miscellaneous activities consisted of all active behaviors which did not fit into any of the previously mentioned behavioral categories. For the sow, the most important component of miscellaneous behavior was caching a caribou carcass during early summer after consuming most of it with her cubs. Caching behavior consisted of 3 periods. In the first, which lasted 52 minutes, the sow began clawing vegetation (mainly tussock grass) about 3 m (10 ft) from the carcass and raking it toward the carcass. She did this first in a northeast direction, then southeast and then southwest and was interrupted. She then moved to about 8 m (25 ft) away and began digging and raking again to cover the carcass. She then ate and rested. Four hours and 30 minutes later she again resumed digging/raking and covering and continued for 53 minutes with only a short break to eat. Four hours and 33 minutes later she again resumed scraping up and raking vegetation and covering the carcass and after 39 minutes was chased away by a large boar. This caching episode(s) made up a little over half of the time the sow spent in miscellaneous behavior over the year and over three-quarters of the time she spent in miscellaneous behavior in early summer.

The next most important category for the sow was made up of unclassified behaviors. The largest component of this category was behavior in which it was impossible to distinguish between borderline feeding and travel. Other examples of behaviors which fell into this category are miscellaneous activities such as nursing or resting, scratching, watching the cubs play, investigating 55 gallon drums, waiting for the cubs, and digging in a snow patch prior to resting in the depression she dug. The

remaining category consisted of time spent by the sow in which she was continuously 'alert' for a half minute or more. It consisted of behaviors in which the sow was either lying or sitting or standing and looking or wandering around and generally scenting the wind. This behavior was mentioned in the section on resting and presumably served to alert the sow to potential dangers or food in her vicinity or was a result of some sight, smell or sound in her vicinity which merited further investigation. Most behaviors of this type did not last even 30 seconds and were not recorded. Behaviors of this type, which lasted 30 seconds or more, made up about 13% of miscellaneous behaviors. Interestingly behaviors in this category seemed to decrease over the year, being highest in spring and early summer seasons, when boars were roaming widely in search of mates and caribou were in the area.

Miscellaneous behaviors of the cubs did not include caching behaviors. The largest category of miscellaneous behaviors for the cubs consisted of behaviors which it was impossible to clearly identify or classify. This category made up 86% of miscellaneous activity for cub 1 and 92% for cub 2. The most important component of this category was also behavior in which it was impossible to distinguish between borderline feeding and travel. Other examples of behavior in this category for the cubs are nursing or resting, nursing attempts or play, running-play or mosquito disturbance, checking unknown objects, checking fuel drums, and rolling on back and looking around. The other category of miscellaneous activity engaged in by the cubs was 'alert' behaviors in which they spent a half minute or more looking around or scenting the air in response to some sight, smell or sound in their vicinity. Alert behaviors of the

cubs appeared to be in response to unusual or food-related stimuli. Unusual stimuli appeared to arouse interest largely for their potential food value. The author appeared to be one such stimuli, which aroused the interest of the cubs. Alert behavior made up about 15% of cub 1's and 8% of cub 2's miscellaneous activity.

## INTRASPECIFIC INTERACTIONS

### Nonagressive Interactions

The sow was observed to feed and rest with other bears in the area without appearing disturbed by their relative proximity as long as they did not approach too directly or closely. Similarly, other bears were not disturbed by the presence of the sow and cubs. Home ranges seemed to be shared amiably in most cases and no instances of territoriality were observed.

### Aggressive Interactions

Interactions of an aggressive nature were observed between the sow and 2 other bears. The most extensive interactions involved the tagged bear Blue-Orange, who was named after the color of the ear tags with which he had been marked by the Alaska Department of Fish and Game. Blue-Orange (B/O) was a 5 1/2 year old male about the same size as the sow and was observed in the vicinity of the sow on 5 separate days. On 2 of these days substantial interactions were noted. On the first of these, on 26 June, B/O was observed resting at 1715 h, 90 m (300 ft) downslope from the resting sow and cubs, who had oriented themselves so they could keep an eye on B/O. The sow still seemed lethargic from being drugged and immobilized on 24 June. Blue-Orange started grazing at 2140 h and approached at one point to within 60 m (200 ft) of the sow. The sow became alert and increasingly nervous as B/O fed closer. Blue-Orange then traveled 90 m (300 ft) upslope to a position about 45 m (150 ft) from the sow and resumed feeding. Less than a minute later at 2311 h

the sow got up and with cubs behind her started walking toward B/O. The sow approached to about 30 m (100 ft) from B/O, stopped, watching him, and then moved forward. Both the sow and B/O now engaged in displacement activity looking around as if for food. When the sow approached to about 25 m (75 ft) from B/O the sow stopped again, both bears facing each other. Now at 2315 h, B/O started walking away and the sow started walking slowly toward him again as though looking around for food. Blue-Orange stopped and looked back and when he saw the sow still moving in his direction, resumed moving away and increased his pace to a fast walk. At 2318 h, the sow turned around and traveled with her cubs back to where they had been resting.

In the interaction which occurred when the sow approached B/O no obvious threats were made other than her direct approach itself. The activity of the sow appeared the same as her normal food search pattern and she did not appear hesitant or nervous. Blue-Orange, however, appeared nervous at her approach. The sow in this instance appeared exceptionally tolerant in letting B/O remain in such extreme proximity to her and her young for such a long period. This may have been partially due to B/O's nonthreatening indirect approach, i.e. feeding around her, only very gradually decreasing the space between and never approaching directly toward her, which might have been construed as threatening. The cubs remained close to the sow throughout the time B/O was near.

Blue-Orange was also observed to interact with the sow on another occasion. On 3 September, the sow was observed walking directly toward B/O; he was walking away. The sow apparently tried to intimidate him into moving off. About a half hour later B/O started walking directly

toward the sow and when he approached to within about 240 to 275 m (800 to 900 ft), the sow started running away with cubs following. The sow and cubs ran for 2 minutes and then continued moving away from B/O at a walk. It seems quite possible that B/O may have been a previous cub of the sow's which might explain her increased tolerance and B/O's tendency to feed near her when she would allow. Blue-Orange was the right age to be an offspring from the sow's last litter and tended to utilize a home range that substantially overlapped the sow's. Both cub 1 and cub 2 were later weaned as 3 year olds in the spring and were observed to remain entirely within the sow's home range when they were on their own, at least during the first year (Reynolds, 1980).

The sow also had a substantial aggressive interaction with a very large male bear of unknown identity. The sow and cubs were resting on the remains of a caribou carcass when cub 1 got up, apparently aware of the nearby large male. A couple minutes later the sow became aware also and quickly fled with her young back toward Meat Mountain, hotly pursued by the boar. The chase was observed for 4 to 4.8 km (2 1/2 to 3 miles) during which time the boar narrowed the gap between itself and cub 2 from 120 m (400 ft) to about 12 to 15 m (40 to 50 ft). Cub 2 continually lagged behind the sow and cub 1 but the apparently terrified sow still repeatedly slowed down for cub 2 to allow her to catch up. Cub 2 repeatedly looked behind at the boar who was steadily gaining on her. The boar loped along at a steady pace behind, his massive frame replete with fat, quivered with every lope and his chest heaved with exertion. At the point where the boar narrowed the lead to 12 to 15 m, the sow and cubs reached the base of Meat Mountain and began running upslope. The sow

slowed further and began running a rear guard position behind the cubs. Then all were hidden by a ridge. The boar appeared 4 minutes later grazing downhill and breathing heavily. Neither the boar, or the sow and the cubs when observed later, appeared injured. It is unknown whether the slope was too much for the heavy, exhausted boar and he gave up at the last minute or whether some aggressive action by the sow deterred him.

I noted a similar instance in Denali National Park, Alaska where a female grizzly ran upslope with her cubs when she was chased by a boar. She finally sent her cubs ahead, faced the boar and attacked him as he approached. Both rose on hind legs wrestling, slapping with forepaws and biting and then shifted to a horizontal position to continue the fight. Shortly thereafter the male broke away and ran off. The female's upslope position seemed to give her the advantage of both height and momentum in the initial clash and may have also made her appear larger and more formidable and intimidating. It is also possible that upslope travel may slow the massive older males to a disproportionately greater degree than the family group and increase the family's chances to escape. Pearson (1975) observed females with spring cubs and yearlings who became separated from their mothers during flight from a threatening situation (helicopter capture) to flee upslope and Stelmock (1981) noted that grizzly families in general moved upslope when disturbed by another bear. Egbert and Stokes (1976) observed that bears at the McNeil Falls in Alaska which were pursued by other bears usually stopped on a crest or promontory to confront their pursuers.

The chase noted of the sow and young in this study from the tundra flats to the slopes of Meat Mountain, up until they were lost from sight, lasted 9 minutes and most of it was at a run. Since the sow was nursing and clearly not in estrus it is unlikely the boar was chasing her to breed and it is almost certain this was an attempt to cannabalize the cubs and possibly the sow. Reynolds (1980) noted one large male in this area to have killed 2, 2-year old cubs belonging to a sow and indicates evidence that it may have also eaten another sow and both her 2-year old offspring; another large male was observed stalking a female with 3 offspring. Reynolds (1980) believed most of the mortality observed in his study, which was also conducted in the NPR-A area, to be attributed to adult males. Intraspecific mortality caused by adult male grizzlies has also been documented elsewhere in Alaska and Canada. Kemp (1976) considered black bear populations in Northern Alberta to be regulated through adult-induced mortality of subadults.

Breeding Interactions

Observations were made of 2 breeding pairs in the Meat Mountain area. One pair consisted of a radiocollared 7 1/2 year old female, #1097, and an unknown blond bear observed on 11 June, 1977 both of which were frightened by my approach and ran off. On 21 June, female #1097 was observed again, and was again near a blond adult, probably the same one, which was identified as a radiocollared 7 1/2 year old male, #1096. Both had been together and were radiocollared at the same time 2 miles northwest of Meat Mountain on 5 June (Reynolds, pers. comm.). This pair was observed for a little over 5 hours. When first observed

at 0900 h, both were resting, lying together. Resting continued until 1130 h (150 minutes) at which time the female got up and started feeding and the male joined her. Feeding continued until 1215 h (45 minutes) at which time the female started traveling west in the direction she had been feeding with the male following about 300 m (1000 ft) behind. By 1255 h, the male and decreased this to 30 m. The male would periodically fall behind and the female would look back to check on him and occasionally wait a little while for him. At 1349 h, another bear followed the pair for 13 minutes before resuming feeding and observations were ended. The pair had traveled for 107 minutes and were still traveling when last observed. The pair bond probably lasted at least 17 days. The female was not observed to be accompanied by cubs the following year (1978) but did have cubs the following spring in 1979, which she lost prior to the breeding season (Reynolds, 1980). Traveling occupied a disproportionate amount of the active time of this sow and blonde male and feeding occupied disproportionately little. In contrast, the longest the sow I studied ever spent traveling was 15 minutes (except for one occasion during the spring recovery period, where she struggled to travel to the cubs while so heavily drugged she could barely stand) and the amount of time spent traveling was very minor compared to the time spent feeding. Travel for the sow also tended to be associated with feeding to a large degree. Reasons for the excessive travel of a mated pair are unclear. Murie (1981) noted similar movements by many mated pairs and also observed pairs that were usually sedentary. He suggests movements are dependent on the particular stage of mating.

Another pair of radio-collared bears was observed by the author to breed on 21 June. The male, #1083, was 7 1/2 years old and had been collared on the upper Utukok River on 25 May. The female, #1085, was 19 1/2 years old and had been collared north of Meat Mountain on 27 May. This female was not observed with cubs the following year in 1978, bred again and was not noted to have cubs in 1979 either (Reynolds, 1980).

## SUMMARY

During 1977, a grizzly bear (Ursus arctos) sow and 2 yearlings were observed periodically on the northern foothills of the Brooks Range of Alaska from shortly after emergence from a den in May through the initiation of denning in October. Each family member was observed for over 350 hours. The bears were active 64% of the time and resting 36% of the time when all observation periods are considered. Seasonally the family was active roughly 14 hours/day in spring, early summer, and late summer, and 17 and 20 hours/day in early fall and late fall respectively.

Activities of the sow over the study consisted of 91.5% feeding/foraging, 0.9% nursing, 4.3% travel, 0.2% play, 0.6% disturbance related and 2.5% miscellaneous behaviors. Activities of the cubs were similar but play occupied about 3.5% of the cubs' active time. Feeding/foraging activities of the sow consisted of 16% digging and consuming roots, 66% grazing or browsing, 15% hunting ground squirrels, 0.2% predation attempts, and about 2% carcass feeding. Feeding/foraging activities of the cubs consisted of 30% digging and consuming roots, 60% grazing or browsing, 3.5% ground squirrel related, 0.2% predation attempts, 2% nursing and 4% carcass feeding. Feeding activites of the family showed marked seasonal shifts.

Digging leguminous roots in which nutrients are stored over winter was almost the exclusive feeding activity of the spring pregreen-up period. Grazing, largely on new growth in which nutrients are concentrated, was the predominant feeding activity in the early and late summer growing seasons (81% and 99%, respectively). In early fall, feeding

activities shifted to digging roots to which nutrients were again being transferred and to browsing on berries where caloric value was concentrated. Around the beginning of early fall fat, nutrient rich ground squirrels became more readily available to the sow. Ground squirrel hunting gradually became the single most important feeding activity of the sow, accounting for roughly 41% of feeding/foraging activity in early fall and 74% in late fall. It has generally been thought that more energy is expended in digging ground squirrels than they provide. This, however, was not the case for the sow in this study. Ground squirrel hunting was probably the single most important food source for the sow during the year, and the sow's caloric intake from ground squirrels alone was estimated at roughly 21,000 kcal/day in the fall. In otherwise marginal habitats, the presence of ground squirrels may be especially important to sows with young and could play a crucial role in the maintenance of some grizzly populations.

The cubs also increased ground squirrel related foraging activity during early and late fall but to a lesser extent than the sow. The yearlings were incapable of digging out ground squirrels on their own and relied mainly on catching ground squirrels escaping past the sow or on stealing them from her. Caloric intake of the cubs from ground squirrels was estimated at 1000 kcal/day in early fall and 1950 kcal/day in late fall. Substantially increased feeding activity during the fall seasons helped the family maximize the utilization of the rich food sources available over much of this time.

A variety of actions by the sow seemed to suggest that much of the sow's behavior from first observations in late May through late June

were oriented toward minimizing contacts with adult male grizzlies who were searching for food and females in breeding condition. Large male grizzlies are often cannabalistic and are thought to be the most important source of mortality among bears in the study area. It appeared, for instance, that the activity cycles of the family during observations in this period might have served to minimize encounters with aggressive male grizzlies at a time when the young may have been particularly vulnerable to predation. Rest sites during this period occurred mainly on barren talus ledges well above the feeding area and appeared to have been selected for their isolation. Home range of the family was extremely small during this time and utilization of this narrow area might have served to minimize encounters with other bears, maintained proximity to safe rest sites, and allowed the family to be near steep slopes in case of pursuit by large boars. The sow was more alert during this period and her rest was more frequently punctuated by monitoring her surroundings (this also was due to the large number of potential prey caribou in the area at the same time). These factors together suggest that care was taken to avoid encounters with large boars at this time. The large number of young, and even an entire family group, which appeared to have been killed and eaten by large males in this area and the very close predatory encounter observed between this family and a large male, suggest good reason for such caution.

Resting by family members usually appeared to take the form of light, easily interrupted sleep. The sow's rest was characterized by periodic monitoring of her environment. Rest sites tended to occur in raised dry places except during the hottest and most mosquito-infested

portion of the summer, during which time snow banks were often sought out. From late May to late June, isolated talus ledges were sought out. During much of the summer and into early fall, a single long rest period typically occurred from early afternoon into the evening. Most rest intervals were much shorter and were spread out over the day. Daily resting period patterns indicated seasonal preferences for rest at certain times of the day but nothing approximating a rigid schedule was observed except for the extended period of rest noted above. Normally all family members rested in close proximity to one another.

The home range of this family group was about 245 $km^2$ (94 $mi^2$) which is similar to that of other grizzly bear sows with young on the North Slope of Alaska, but substantially larger than observed for grizzly females elsewhere. Home range use during most seasons centered around areas where (apparently) there was a higher availability of particular food sources than in the remainder of the home range, and similarly at times because of the availability of particular resting sites. Centers of activity changed seasonally with phenology, availability of food sources, and changing rest site requirements. Centers of activity from late June on, were often quite large and considerable movement occurred. More widespread feeding (both inside and outside of the activity centers) was advantageous in that it allowed the sow and cubs to thoroughly familiarize themselves with the area, enhanced location of ground squirrel burrows, maximized chance encounters with particularly high value food sources, such as carrion, nesting birds, eggs, feeding ground squirrels and microhabitats with preferred vegetation, and minimized damage to any one particular feeding area.

Travel by the sow consisted primarily of movements between feeding sites (83%) and secondarily of travel to and from resting sites (13%). Travel by the young was almost entirely oriented toward maintaining proximity to the sow. Normally, proximity to the sow was maintained simply by orienting feeding activity toward the sow. However, if the sow was observed to travel, the cubs would travel also. Or if distance between the sow and cubs reached critical levels for one reason or another, the cubs would travel to catch up to her. The responsibility for maintaining proximity between sow and cubs appeared almost wholely delegated to the cubs who monitored the position of the sow in relation to themselves. Proximity between cubs appeared to be mutually maintained almost entirely through oriented feeding activities and only very rarely involved travel.

Nursing behaviors were observed in this study from first observations in late May through the third week in August. The sow nursed her young an average of 4.8 minutes per nursing bout and bouts ranged from 2 to 7 minutes in length. During the observed nursing season, the sow and cubs were engaged in nursing 1% of the observation time and nursing accounted for 1.5% of the feeding activity of the cubs. Frequency of nursing was 3.3 bouts per day. Nursing was a substantial energy drain on the sow and an important supplement for the young. The sow's energy output in milk was estimated to be 3300 kcal/day. Nursing the young in the spring probably resulted in a substantial weight loss for the sow over this period because she was supporting herself and supplementing the young with high protein, fat, and minerals drawn almost entirely from her remaining overwinter reserves. Around mid-August, nursing

either ceased or was severely reduced for the year as berries and ground squirrels became available and reduced the need for milk supplements. A shift in activity patterns, an increase in activity levels, an increase in movements, an increase in home range size, and a substantial increase in sow-cub, but not cub-cub, average distance, occurred at the same time as the apparent end to or possible severe reduction of nursing, and were probably indirectly related to it; all of these factors appeared to reflect a general overall pattern of preparation of reserves for hibernation. The increased activity, movements, and home range size reflected the increased foraging behaviors; cessation of nursing allowed the sow to reduce the heavy energy and nutrient drain of lactation at a time when berries became abundant and were readily available to build the cubs' fat reserves; and increased sow-cub but not cub-cub distance appeared to reflect the sow's substantially increased movements and possibly the end of nursing.

Dates of latest observed nursing or lactation in the literature suggest that grizzly sows with young typically cease nursing their young in August or September. The literature also has numerous observations of sows observed to nurse the same young again the following spring, as was the case with the sow in this study. Strong circumstantial evidence from a variety of sources supports the hypothesis that sows which keep their young an additional year do not nurse them at all during the winter or do so only very rarely, contrary to what has been thought, conserving this costly energy expenditure for spring when it is needed most.

Of the nursing bouts where an initiator was known, the sow initiated slightly over half, the cubs acting together initiated slightly over a third, and the remainder were initiated by a single cub. Nursing attempts in which both cubs joined forces, while much fewer in number than isolated attempts, were far more successful. Attempts to nurse ranged in intensity from a low-keyed maintainence of proximity to the sow, to outright harassment involving repeated pawing or nuzzling or repeated direct attempts to simply grab a teat. Nursing attempts were typically rebuffed by the sow ignoring them or by turning over, turning away, or walking off. When nursing, the sow typically laid on her back. When the sow nursed from this position, cub 1 always nursed from the right side and cub 2 from the left side. Roughly 80% of the nursing bouts were found to be associated with rest periods. Activity associated nursing bouts were also found to be significantly shorter than resting associated nursing bouts for the sow at the 1% level. Of those bouts where the terminator(s) was known, nearly one third involved termination of both cubs by the sow, one quarter involved termination of one cub after the other cub had finished nursing, and in nearly half of the events both cubs were allowed to nurse until done. To terminate a bout, the sow simply turned over or walked off.

Over the year, 130 play events were observed. These consisted of 4 types: solitary play, play-fighting, play-running, and mixed play-fighting and play-running. Play events took place mostly between the cubs. Duration of play involving only the cubs averaged 3.7 minutes. Play events ranged in duration from 10 seconds to 28 minutes. Play involving the cubs averaged 10 occurrences/day. Play was least frequent

prior to the vegetation growing season when environmental conditions were poor and most frequent in early summer when frequency of play averaged 25 occurrences/day. Over the year, play-fighting made up 75% of the cub's play, play-fighting mixed with play-running made up 17%, solitary play 6%, and play-running 2%. Solitary play, however, is probably substantially under-represented in these percentages due to difficulty at times in clearly identifying it. Frequencies of these types of play suggest a gradual seasonal shift in the proportion of social play types observed; from largely play-fighting in early summer, to mostly mixed play-fighting and play-running, and pure play-running, by late fall.

A variety of motor patterns were used to initiate social play and each cub appeared to have favorite individual methods of doing so. In contrast, motor patterns of actual play interactions tended to be much more uniform between the cubs although slight preferences still existed. Motor patterns of play-fighting consisted largely of biting, jaw wrestling, boxing (swatting), and body wrestling. Attacks seemed predominantly oriented to the head, neck, and shoulder regions with greatest emphasis on the head. Motor patterns of play-running consisted of chases and of running around together. Solitary play consisted predominantly of a cub running around by itself.

Play seemed to be strongly characterized by the young learning about themselves and their environment, and by the development of motor skills such as play-fighting and running which enhanced survival in their environment. Skills developed in play-fighting enhanced their chances of winning aggressive encounters as adults, and skills developed

in play-running and chase enhanced motor skills used in escaping life threatening encounters (such as from large boars) and in catching prey. While play behaviors of the barren-ground grizzly bear young in this study appeared to be similar to that observed in black bear young, the differences which exist reflected their differing environments and lifestyles. Differences existed for instance, in object play, which was particularly important to black bears who climb trees for protection and food, manipulate branches and overturn logs for food and have a considerable variety of objects to manipulate in their environment. In the barren-ground grizzly bear's environment, such objects are less common and less important, and object play was not observed. (Object play has been noted in grizzly young in more intermediate environments.) Other differences between the barren-ground grizzly young and black bear young include a lack of climbing play in the grizzly (who have no trees to climb) and a lack of solitary running-play in the black bear. Differences between play in barren-ground grizzly and black bear young also appear in the duration of such bouts and the intervals between these bouts. Play bouts between the grizzly young observed in this study lasted much longer on the average than play bouts observed between black bear young and these differences may be species specific. Intervals between bouts were longer in grizzly bear young and shorter in black bear young but may reflect black bear young being well fed and in captivity while the wild grizzly young had to devote substantial amounts of time to foraging for themselves so bouts were less frequent.

A limited number of instances (n = 16) of aggressive attacks between family members were observed. Attacks lasted from 1 to 12 seconds

and averaged about 5 seconds. Attacks between the young were associated primarily with prized foods of limited availability. Attacks by the sow were associated with both prized foods and with aggressive behavior by the cubs. Attacks between the cubs were more frequent than attacks involving the sow and a cub. Attacks between the cubs averaged once every 24 hours. Attacks appeared to occur abruptly without elaborate motor patterns signaling threat. Threat appeared to be expressed by more subtle body language and vocalizations that were difficult to identify at a distance. Attacks between cubs were usually initiated by 1 cub suddenly lunging at the other. Attacks were typically composed of hard fast slugging combinations using the forepaws or slugging combinations mixed with bites. The attacked cub either would back away rapidly, assuming a defensive posture, sometimes slugging back while extricating itself, or attack in return with a brief fight ensuing. If the former, once the attacked cub had succeeded in extricating itself, the attacker would almost immediately resume his former activity, terminating the interaction. If a fight occurred it was similarly terminated by the cubs separating, backing away a safe distance out of range of a surprise attack, stopping momentarily to watch each other and then walking off and assuming other activities. Aggressive attacks usually resulted in little or no apparent benefit to the aggressor. Attacks between the young often appeared to be actively or passively discouraged by the sow. Motor patterns of aggressive attacks were easily distinguished from similar motor patterns of play by their extreme speed, intensity of bites and swipes, shortness of duration, and the context in which they occurred. Aggressive attacks appear to have been substantially shorter

in the grizzly yearlings than in similar aged captive black bear young, possibly due to discouragement by the mother in the case of the grizzly young.

A number of disturbances to the family group were noted, most of which were due to the presence of aircraft. The reaction elicited appeared to be a function of the noise level reaching the sow. The closer the approach, the greater the noise level and the more intense the reaction. At very close approaches, there appeared to be a negative visual impact as well, and such approaches normally resulted in panic running by the sow and cubs. Simple awareness of human presence in the area could also cause severe disturbances. Natural disturbances included close approaches by other bears and an instance of a predation attempt on the family by a large boar.

A less severe but more persistent source of disturbance to the family appeared to be mosquito harassment which began around late June and lasted until late July. Movements increased, the family group spread out much further from one another, the sow fed in a highly erratic pattern at a fast walk, stationary feeding behaviors such as nursing and digging for ground squirrels were greatly reduced, snowbanks and creek-beds were sought out as havens, and occasional instances of non-play running by the cubs was observed which appeared to be related to harassment. These behaviors are similar to those observed in caribou subjected to moderate levels of mosquito harassment.

## LITERATURE CITED


Banfield, A.W.F. 1958. The distribution of the Barren-Ground grizzly bear in northern Canada. Natl. Mus. Can. Bull. 177:47-59.

Banfield, A.W.F. 1964. Grizzly territory. Nat. Hist. 73(3):23-27.

Beckoff, M. 1972. The development of social interaction, play, and metacommunication in mammals: an ethological perspective. Quart. Rev. Biol. 47:412-434.

Bromlei, F.G. 1965. Bears of the south far-eastern U.S.S.R. 1973. Translation. Published for the U.S. Dept. Interior, Bureau of Sport Fisheries and Wildlife and National Science Foundation, Washington, D.C., by the Indian National Scientific Documentation Centre, New Dehli, TT70-57215. 138 pp.

Burghardt, G.M. and L.S. Burghardt. 1974. Notes on behavioral development of two female black bear cubs: their first eight months. Pages 207-220 in S.M. Herrero, ed. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 23. Morges, Switzerland.

Carl, E.A. 1971. Population control in arctic ground squirrels. Ecology 52(3): 395-413.

Conover, W.J. 1971. Practical nonparametric statistics. John Wiley and Sons, New York. 462 pp.

Craighead, F.C. 1976. Grizzly bear ranges and movement as determined by radio tracking. Pages 97-110 in: M.R. Pelton, J.W. Lentfer, and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Craighead, F.C. and J.J. Craighead. 1972. Grizzly bear prehibernation and denning activities as determined by radio tracking. Wildlife Monographs No. 32. 35 pp.

Craighead, F.C. and J.J. Craighead. 1973. Tuning in on the grizzly. Science Year: The World Book Annual (Field Enterprises Educational Corp., Chicago) 1973:34-49.

Craighead, F.C. and J.J. Craighead. 1974. Data on grizzly bear denning activities and behavior obtained by using wildlife telemetry. Pages 84-106 in: S.M. Herrero, ed. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 23. Morges, Switzerland.

Craighead, J.J. and J.S. Sumner. 1980. Grizzly bear habitat analysis. Section II: Evaluation of grizzly bear food habits, food plants, and habitat. University of Montana, Missoula. Unpubl. 157 pp.

Crook, J.L. 1971. Determination of abundance and distribution of brown bear (Ursus arctos) north of the Brooks Range, Alaska. M.S. Thesis. University of Alaska, Fairbanks. 78 pp.

Curry-Lindahl, K. 1974. The brown bear (Ursus arctos) in Europe: decline, present distribution, biology and ecology. Pages 74-80 in S. Herrero, ed. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 23. Morges, Switzerland.

Dean, F.C. 1957. Investigations of grizzly bears in Interior and Arctic Alaska. Rept. No. 1., work done in Mt. McKinley National Park, 1957. Rept. to Arctic Institute of No. Am. Unpubl. 40 pp.

Durnin, J.V.G.A. and R. Passmore. 1967. Energy, work, and leisure. Heinemann Educational Books, London. 166 pp.

Egbert, A.L. and A.W. Stokes. 1976. The social behavior of brown bears on an Alaskan salmon stream. Pages 41-56 in M.R. Pelton, J.W. Lentfer, and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Eibl-Eibesfeldt, I. 1970. Ethology, the biology of behavior. Holt, Rinchart and Winston, New York. 530 pp.

Folk, G.E., A. Larson, and M.A. Folk. 1976. Physiology of hibernating bears. Pages 373-380 in M.R. Pelton, J.W. Lentfer, and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Fox, M.W. 1971. Behavior of wolves, dogs and related canids. Harper and Row Publishers, Inc., New York. 220 pp.

Galster, W. and P. Morrison. 1976. Seasonal changes in body composition of the arctic ground squirrel. (Citelus undulatus). Can. J. Zool. 54:74-78.

Hanwell, A. and M. Peaker. 1977. Physiological effects of lactation on the mother. Pages 297-312 in M. Peaker, ed. Comparative aspects of lactation. Symp. Zoo. Soc. Lond. No. 41. Pub. for the Zoological Society of London by Academic Press, London.

Hechtel, J. 1979. Behavioral ecology of a barren-ground grizzly bear female and her young in the National Petroleum Reserve - Alaska. Preliminary Report, Montana Cooperative Wildlife Research Unit, Missoula. 11 pp.

Henry, J.D. and S.M. Herrero. 1974. Social play in the American black bear: Its similarity to canid social play and an examination of its identifying characteristics. Am. Zool. 14:371-391.

Hensel, R.J., W.A. Troyer, and A.W. Erickson. 1969. Reproduction in the female brown bear. J. Wildl. Mgmt. 33(2):357-365.

Jenness, R., A.W. Erickson, and J.J. Craighead. 1972. Some comparative aspects of milk from four species of bears. J. Mammal. 53(1):34-47.

Jordan, R.H. 1976. Threat behavior of the black bear (Ursus americanus). Pages 57-63 in M.R. Pelton, J.W. Lentfer and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Kemp, G.A. 1976. The dynamics and regulation of black bear (Ursus americanus) populations in northern Alberta. Pages 191-197 in M.R. Pelton, J.W. Lentfer and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Kiell, D.J. and J.S. Miller. 1980. Reproduction and nutrient reserves of arctic ground squirrels. Can. J. Zool. 58:416-421.

Kingsley, M.C., J.A. Nagy and R.H. Russell. In Press. Patterns of weight gain and loss for grizzly bears in Northern Canada. Presented at the Fifth Int. Conf. on Bear Research and Mgmt., Madison, Wisconsin. Feb. 10-13, 1980.

Kleiber, M. 1961. The fire of life: an introduction to animal energetics. John Wiley and Sons, Inc., New York. 454 pp.

Krementz, A. 1888. Der Bär (The Bear). Berlin.

Krott, P. 1964. Bears in the family. E.P. Dutton and Co., Inc., New York. 144 pp.

Lloyd, L.E., B.E. McDonald and E.W. Crampton. 1978. Fundamentals of nutrition. 2nd ed. W.H. Freeman and Co., San Francisco. 466 pp.

Mayer, W.C. and E.T. Roche. 1974. Development patterns in the Barrow ground squirrel, Spermophilus undulatus barrowensis. Growth 18:53-69.

Mealey, S.P. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973-74. Pages 281-292 in: C.J. Martinka and K.L. McArthus, eds. Bears - their biology and management. Bear Biol. Assoc. Conf. Ser. U.S. Gov. Printing Off.

Meyer-Holzapfel, M. 1957. Das verhalten der baren (Ursidae). Handbuch Zool. 8(10):1-28.

Miller, L. 1972. Panel discussion on bear behavior. Pages 243-254 in: S. Herrero ed. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Series No. 23. Morges, Switzerland.

Murie, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States, Fauna Ser. No. 5. U.S. Gov. Printing Office, Washington, D.C. 238 pp.

Murie, A. 1952. Grizzly mothers in the Alaska Range. The Living Wilderness. 17(42):15-21.

Murie, A.J. 1981. The grizzlies of Mount McKinley. National Park Service Monogr. Ser. No. 14. 251 pp.

Nelson, R.A. 1978. Urea metabolism in the hibernating black bear. Kidney International 13 (Suppl. 8): S 177- S 179.

Nelson, R.A. 1980. Protein and fat metabolism in hibernating bears. Fed. Proc. 39(12):2955-2958.

Nelson, R.A., G.E. Folk, E.W. Pfeiffer, J.J. Craighead, C.J. Jonkel, and D.M. Wellik. In Press. Behavior and biochemical adaptation of black, grizzly and polar bears. Presented at the Fifth Int. Conf. on Bear Research and Mgmt. Madison, Wisconsin. Feb 10-13, 1980.

Nelson, R.A., H.W. Wahner, J.D. Jones, R.D. Ellefson, and P.E. Zollman. 1973. Metabolism of bears before, during and after winter sleep. Am. J. Physiol. 224:491-496.

Pearson, A.M. 1975. The northern interior grizzly bear (Ursus arctos). Can. Wildl. Serv. Rept. Series No. 34, Ottawa. 86 pp.

Pearson, A.M. 1976. Population characteristics of the Arctic mountain grizzly bear. Pages 247-260 in: M.R. Pelton, J.W. Lentfer and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Pruitt, C.H. 1974. Social behavior of young captive black bears. Ph.D. Thesis. University of Tennessee, Knoxville. 137 pp.

Pruitt, C.H. 1976. Play and agonistic behavior in young captive black bears. Pages 79-86 in M.R. Pelton, J.W. Lentfer and G.E. Folk, eds. Bears - their biology and management. Int. Union Conserv. Nat. Nat. Resources Publ. New Ser. No. 40. Morges, Switzerland.

Pruitt, C.H. and G.M. Burghardt. 1977. Communication in terrestrial carnivores: mustelidae, procyonidae, and ursidae. Pages 83-107 in T. Sebeok, ed. How animals communicate. Indiana University Press. Vol. 2.

Quimby, R. 1974. Grizzly bear. Arctic Gas. Biol. Rep. Ser. No. 24, Capt. 2. 97 pp.

Reynolds, H. 1974. North Slope grizzly bear studies. Alaska Dept. Fish and Game, Fed. Aid Wildl. Rest. Rep. Proj. W-17-6, Jobs 4.8 R-4.11 R, Juneau. 27 pp.

Reynolds, H. 1976. North Slope grizzly bear studies. Alaska Dept. Fish and Game, Fed. Aid. Wildl. Rest. Rep. Proj. W-17-6 and 7, Jobs 4.8R-4.11R, Juneau. 22 pp.

Reynolds, H. 1980. North Slope grizzly bear studies. Alaska Dept. Fish and Game. Fed. Aid. Wildl. Rest. Project No. W-17-11, Job No. 4.14 R. 65 pp.

Schallenberger, A. 1980. Review of oil and gas exploration impacts on grizzly bears. Pages 271-276 in C.J. Martinka and K.L. McArthus, eds. Bears - their biology and management. Bear Biol. Assoc. Conf. Ser. U.S. Gov. Printing Off.

Searby, H.W. 1971. Climate of the North Slope, Alaska. U.S. Dept. of Commerce, N.O.A.A. Technical memorandum, AR-4. 54 pp.

Selkregg, L.L. 1975. Alaska Regional Profile - Arctic Region. Arctic Environmental Information and Data Center, Univeristy of Alaska, Anchorage. 218 pp.

Servheen, C. and L.C. Lee. 1979. Mission Mountains grizzly bear studies: an interim report. 1976-78. Border Grizzly Project, University of Montana, Missoula. BGP Spec. Rept. No. 31. 229 pp.

Sizemore, D. 1980. Foraging strategies of the grizzly bear as related to its ecological energetics. M.S. Thesis. University of Montana, Missoula. 67 pp.

Spetzman, L.A. 1959. Vegetation of the Arctic Slope of Alaska: U.S. Geological Survey Professional Paper 302-B, pages 19-58.

Stelmock, J.J. 1981. Seasonal activites and habitat use patterns of brown bears in Denali National Park - 1980. M.S. Thesis. University of Alaska, Fairbanks. 118 pp.

Stonorov, D. 1972. Protocol at the annual brown bear feast. Nat. Hist. 81(9):66-73, 90-94.

Stonorov, D. and A. Stokes. 1974. Social behavior of the Alaskan brown bear. Pages 232-242 in S.M. Herrero, ed. Bears - their biology and management. Int. Union conserv. Nat. Nat. Resources Publ. New Ser. No. 23. Morges, Switzerland.

Tembrock, G. 1958. Spielverhalten beim Rotfuchs. Zool. Beitr. Berlin 3:423-496.

Thomson, B.R. 1977. The behavior of wild reindeer in Norway. Ph.D. Thesis. University of Edinburgh, Scotland. 429 pp.

Troyer, W.A. and R.J. Hensel. 1962. Cannabalism in brown bear. Anim. Behav. 10:231.

Troyer, W.A. and R.J. Hensel. 1969. The brown bear of Kodiak Island. U.S. Dept. of Interior, Bureau of Sport Fisheries and Wildlife, Branch of Wildlife Refuges, Kodiak National Wildlife Refuge, Kodiak, Alaska. Unpubl. 233 pp.

U.S. Dept. of the Interior. 1978a. National Petroleum Reserve in Alaska, Physical Profile. U.S. Dept. of Interior. 124 pp.

U.S. Dept. of the Interior. 1978b. National Petroleum Reserve in Alaska, Ecological Profile. U.S. Dept. of Interior. 118 pp.

Vorherr, H. 1974. The breast. Morphology, physiology, and lactation. Academic Press, New York. 282 pp.

White, R.G., B.R. Thomson, T. Skogland, S.J. Person, D.E. Russell, D.F. Holleman and J.R. Luick. 1975. Ecology of caribou at Prudhoe Bay, Alaska. Pages 151-201 in J. Brown, ed. Ecological investigations of the Tundra Biome in the Prudhoe Bay region, Alaska. University of Alaska Biological Papers, Special Report No. 2.